3

POPULATION STRUCTURE AND THE INFECTION BIOLOGY OF WOOD-DECAY FUNGI IN LIVING TREES

A. D. M. Rayner[1] and Lynne Boddy[2]

[1] *School of Biological Sciences, University of Bath, Claverton Down, Bath, Avon, England*

[2] *Department of Microbiology, University College, Newport Road, Cardiff, S. Glamorgan, Wales*

I. Principles 119
A. Population Studies and the Aetiology of Infection 119
B. Decay and Disease in Living Trees 120
C. The Tree as a Selective Environment 120
D. Generation of Variation 121
E. Somatic Incompatibility and the Delimitation of Individual Genotypes 123
II. Modes of Arrival 127
A. Arrival by Mycelium 128
B. Arrival by Propagules 129
III. Modes of Entrance and Establishment: Invasion Strategies . . . 132
A. Heartrots 132
B. Colonization of Disrupted Sapwood 135
C. Colonization of Intact Sapwood 141
IV. The Problem of Selectivity: Adaptation and Ecodifferentiation . . 149
A. Occurrence and Possible Causes of Selectivity 149
B. Adaptation, Diversification and the Correlation between Reproductive and Ecological Strategies 154
References 157

I. PRINCIPLES

A. Population Studies and the Aetiology of Infection

It is widely accepted that the presence of genetic variation within pathogen populations may be associated with differences in virulence and host-

Advances in Plant Pathology, Vol. 5
ISBN 0-12-033705-3

Copyright © 1986 Academic Press Inc. (London) Limited
All rights of reproduction in any form reserved

specificity between different individuals or groups. Furthermore, since the distribution within and between hosts of particular pathogen genotypes must be a direct reflection of their patterns of spread and establishment, it is clear that knowledge of the spatiotemporal genetic structure of pathogen populations will provide a deeper understanding of disease aetiology. This will also be evident from the discussion of the population structure of *Ceratocystis ulmi* by Brasier in this volume. Our purpose here will be to discuss what is known, and what needs to be known, about the relationship between population structure and the infection biology of fungi causing decay of wood in living trees. It will soon become apparent that the relative lack of information available in certain critical areas forces us to speculate about possibilities. However, it is hoped that these overt speculations, combined with the real evidence which is already available, will provide a framework of ideas enabling further progress to be made, and which can be discarded or accepted as suitable evidence accumulates.

B. Decay and Disease in Living Trees

There is often debate as to whether or not decay of the wood should truly be regarded as a disease in trees. This particularly applies to heartwood where few or no living cells are present, but even in sapwood, living cells often account for less than 10% of volume (Hillis, 1977). Fungal colonization may therefore effectively be of predominantly dead tissue, and although access to this tissue may be via direct pathogenesis, as will be described below, it is often difficult to distinguish between primary and secondary effects. However, from a practical standpoint, and since the pioneering studies of Hartig (1874, 1878), decay in standing trees has long been considered a major source of economic loss and of direct concern to forest pathologists. We make no apology therefore for including fungi exhibiting a wide range of colonization strategies in the following discussion, regardless of whether or not direct pathogenesis is involved. We will, however, mostly restrict ourselves to cases where the decay fungi can be regarded as primary colonizers rather than secondary invaders of already diseased or dead timbers.

C. The Tree as a Selective Environment

A cornerstone of our agument is the fact, virtually a truism, that the living tree imposes considerable selection pressures militating against invasion of its interior: these are due primarily to limitation of accessibility by the presence or production of physico-chemical barriers and secondarily to the hostile micro-environmental conditions which may obtain once these barriers are breached.

Physico-chemical barriers limiting access to the interior include the suberized tissues of bark, abscission zones and similar, together with gums, resins and tyloses which seal off injured from intact sapwood. Hostile microenvironmental conditions can be due to the presence of allelopathic chemicals, including the toxic extractives which characterize some heartwoods and regions abutting injured sapwood (Scheffer and Cowling, 1966; Hillis, 1977). Absence of readily assimilable nutrients, unfavourable gaseous regimes and—particularly in sapwood—water saturation limiting exchange of oxygen and carbon dioxide across long diffusion paths, introduce further stresses (Boddy and Rayner, 1983a; Cooke and Rayner, 1984). Such stresses must be tolerated, optimized or circumvented if successful mycelial development and consequent oxidative decay processes are to be initiated, and this effectively provides the basis for the range of colonization strategies exhibited by decay fungi in trees.

D. Generation of Variation

As in other eukaryotes, population variation amongst wood decay fungi is predominantly generated and maintained by systems of sexual outcrossing. This latter involves conjugation (plasmogamy) between genetically different individuals culminating in nuclear fusion (karyogamy), meiosis and recombination, and in heteromictic (heterothallic) fungi is controlled by a variety of genetic mechanisms, broadly known as mating systems.

In Ascomycotina dimictic mating systems occur: these are controlled as though by a single bi-allelic locus (Burnett, 1975, 1976). This effectively divides the entire breeding population (as well as sib-related progeny from the same ascocarp or fruit body) into two different types of individuals (mating types) between which fertilization resulting in production of viable ascospores can occur, but which are individually self-sterile (Brasier, this volume). Because of the presence of only two types of individual, outcrossing (as defined above) is imposed, but there is no intrinsic bias for outbreeding (fertilization between non-sib as opposed to sib-related lines).

By contrast, in Basidiomycotina (excepting Hemibasidiomycetes) diaphoromictic mating systems occur, which are controlled by one, two or perhaps exceptionally three (hence unifactorial, bifactorial, trifactorial) mating-type factors, each of which is multi-allelic. Thus, although sib-related progeny from a single basidiocarp (fruit-body) are of two, four or eight mating types (hence bipolar, tetrapolar or octopolar mating systems), many mating types occur in the breeding population as a whole, resulting in an intrinsic outbreeding bias imposed by the genetic system (Burnett, 1975, 1976).

A further difference between outcrossing populations of Ascomycotina and Basidiomycotina is that, in the former, conjugation typically involves sexually

differentiated organs and mating-type heterokaryons are restricted to the ascogenous hyphae. By contrast, in the Homobasidiomycetes and some Heterobasidiomycetes, conjugation is between somatic hyphae of haploid homokaryons (primary mycelia developing by germination of basidiospores) and results in production of a stable secondary mycelium which is heterokaryotic, containing two types of nuclei differing in mating type.

However, outcrossing is not necessarily imposed in many Ascomycotina and Basidiomycotina populations. Firstly, the widespread facility for asexual reproduction via mycelial fragmentation or conidium production readily results in clonal populations. Secondly, the production of ascospores and basidiospores need not always follow conjugation between complementary mating types. This can be due to any of several phenomena including the following: homomixis or primary homothallism (self-fertility of a haploid homokaryon); homoheteromixis or secondary homothallism (production of binucleate ascospores or basidiospores heterokaryotic for mating type); homokaryotic fruiting and mitotic production of basidiospores; amixis or apomixis. With the exception of homoheteromixis (which can be regarded as imposing inbreeding) these all result in production of clonal progeny sets because of lack of the opportunity for recombination in a haploid homokaryon, and hence can perhaps be considered equivalent in population terms. It may also be noted that, whereas homomixis does not necessarily prevent outcrossing in those Ascomycotina which have sex organs, imposition of a homomictic or amictic system in Basidiomycotina does preclude outcrossing because of somatic incompatibility (see Section I.E) between different homokaryotic lines. The latter situation, which occurs for example in *Stereum sanguinolentum*, must therefore be carefully distinguished from the simple ability of homokaryons to fruit in outcrossing populations, the crucial feature here being whether or not a mating system controlling heterokaryosis is present (Rayner and Turton, 1981; Rayner *et al.*, 1984; see also below).

Besides normal outcrossing, other sources of variation must also be considered as of potential significance in wood-decay populations. These include somatic mutations and the possibility of heterokaryosis and parasexuality arising by vegetative anastomoses between non-mating-type compatible strains. However, there is increasing evidence (see also Brasier, this volume) that such parasexuality is effectively limited to virtually isogenic lines as a result of somatic incompatibility mechanisms.

Developmental variation, resulting from different patterns of regulation of gene expression, perhaps sometimes via transposable elements, is also likely to be significant and may account for the sometimes striking switches in morphogenesis (changes of "mode"; see Gregory, 1984) exhibited by wood-decay fungi (Fig. 1) and which provide a basis for response to changing demands as the resource changes during heterotrophy. In this context it is

worth mentioning recent evidence implicating a single, transmissible regulatory switching element, whose activity can generate remarkable variation in mycelial and reproductive differentiation in the wood-decaying basidiomycete *Stereum hirsutum* (Coates and Rayner, 1985a, 1985b). The role of cytoplasmic elements including plasmids, double-stranded RNA and mitochondrial DNA (see also Brasier, this volume) must also be considered, as must the possibility of heteroploidy and polyploidy (Tolmsoff, 1983).

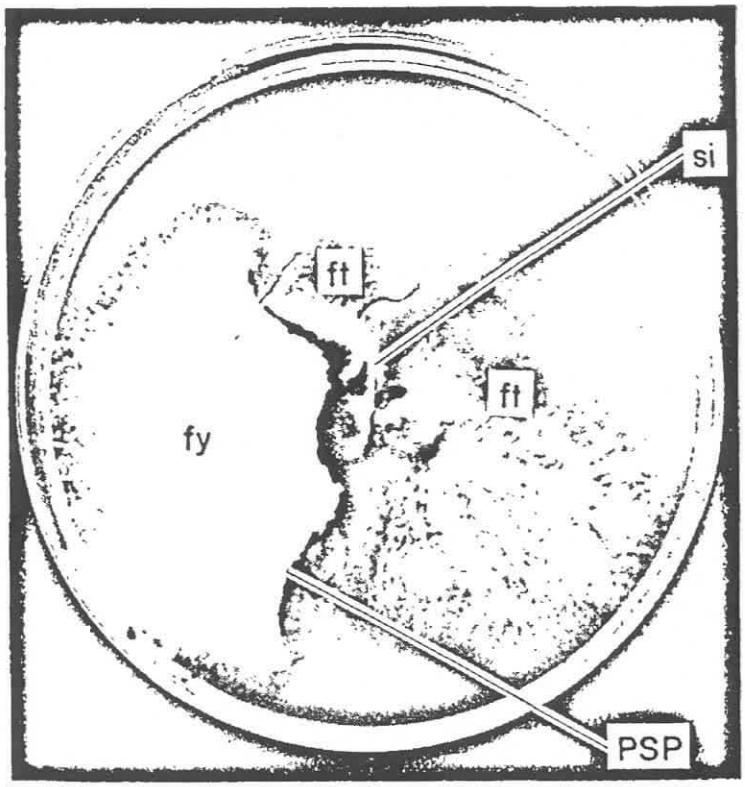

Fig. 1 A paired culture between two isolates of *Hymenochaete corrugata* showing the two different mycelial morphologies, 'flat' (ft) and 'fluffy' (fy). Note the zone of somatic incompatibility (si) between the two mycelia, the occurrence of ft morphology adjacent to the interaction line, and the formation of a pseudosclerotial plate (PSP) between the ft and fy phases in the colony on the left. (Reproduced with kind permission from P. R. Sharland.)

E. Somatic Incompatibility and the Delimitation of Individual Genotypes

1. Occurrence and Timing

It is now widely recognized that in genetically variable populations of Ascomycotina and Basidiomycotina, somatic (=vegetative) incompatibility, a self/non-self rejection mechanism (Fig. 2), operates to delimit individual genotypes from one another and to reduce the scope for genetic and

physiological collectivism between them (Rayner *et al.*, 1984; see also Brasier, this volume). The mechanism appears to depend on the presence of genetic differences at the somatic incompatibility loci, which being polygenic or multiallelic ensure that, although not inevitable, rejection is the rule between adjacent thalli of different genotypes in extensively outcrossing populations.

A major difference between outcrossing Ascomycotina and Basidiomycotina is that in the former, somatic incompatibility is directly expressed between haploid homokaryons—which in these fungi constitute the predominant vegetative phase. By contrast, in the somatogamous outcrossing Basidiomycotina somatic incompatibility is expressed between secondary mycelia, and sometimes between non-mating-compatible homokaryons, but not, or only *temporarily*, between mating-compatible homokaryons where production of the heterokaryotic secondary mycelium is imperative. This situation has given rise to the concept that mating-compatible homokaryons of Basidiomycetes *override* the somatic rejection response (Rayner and Todd, 1979; Rayner and Turton, 1982; Rayner *et al.*, 1984; Coates, Rayner and Boddy, 1985).

Fig. 2. Somatic incompatibility between two isolates of *Stereum gausapatum*. Dark-red liquid droplets were exuded in the interaction zone.

The basis for override cannot be discussed in detail here, but probably involves several mechanisms concerning the migration and stable association of complementary nuclei of which three have been proposed: *access* migration, *acceptor* migration and *stabilization* (Rayner *et al.*, 1984). *Access* migration allows ingress of donor nuclei into an acceptor mycelium at a rate dependent on the genetic relationship between donor and acceptor so that asymmetric or unilateral migration patterns are commonly observed. Acting alone, it results

in abnormal branching and inhibition of colony extension and donor nuclei may migrate predominantly via lateral fusions between hypae. *Acceptor* migration, which is dependent on an initial access step, occurs via pre-existing hyphae (and hence necessarily through septa) at a rate determined by the acceptor only. *Stabilization* allows the production of a heterokaryon in which the complementary nuclei are stably associated.

Although override is not prerequisite for outcrossing in gametangiogamous Ascomycotina, there is evidence in certain xylariaceous wood-decaying species that at least the access phase may operate, resulting in temporary heterokaryosis and, often, an eventual territorial gain by one partner in paired combinations. Thus in *Daldinia concentrica*, 'bow-tie-shaped' interaction zones—analogous to those seen in many Basidiomycotina (Fig. 3a; Coates, Rayner and Todd, 1981)—often develop between paired single ascospore, wood or stromatal isolates, in which there is profuse development of white aerial mycelium (Fig. 3b). On subculture the latter usually breaks down into one or other (or occasionally both) of its homokaryotic components. A somewhat similar situation occurs in *Hypoxylon fuscum* (Fig. 3c) and *Hypoxylon serpens* (Fig. 3d) where an apparently heterokaryotic mycelium, unstable on subculture, develops from somatic incompatibility zones and effectively overrides the rejection response. Here, the only differences from basidiomycete behaviour are lack of stabilization and occurrence between all monosporous sibs rather than between complementary groups (i.e. mating types). Whether or not these access phenomena are related to the penetration effect described by Brasier (1984 and this volume) in *Ceratocystis ulmi* is not resolved.

Finally, it must be noted that in certain Basidiomycotina, such as *Stereum sanguinolentum* (see below), which lack an outcrossing mechanism, somatic incompatibility is expressed directly between different homokaryotic lines forming clonal or near-clonal sub-populations.

2. *Effects on Domain*

For wood, the usual manifestation of somatic incompatibility within decay species is the development of relatively undecayed interaction zone lines between decay columns occupied by adjacent thalli (Fig. 4). Intriguingly, these lines, which are really narrow regions of wood only appearing as lines in cross-section, frequently provide a niche for certain dematiaceous microfungi which are not active decomposers (Rayner, 1976). The presence of the lines indicates a very important feature, the mutual exclusivity of individual genotypes and the consequent restriction of domain occupied by each when they are concurrent.

Mycelial domain is in turn related to the eventual reproductive commitment of an individual and activity in resource utilization; thus when colonization occurs under circumstances allowing the concurrence of numer-

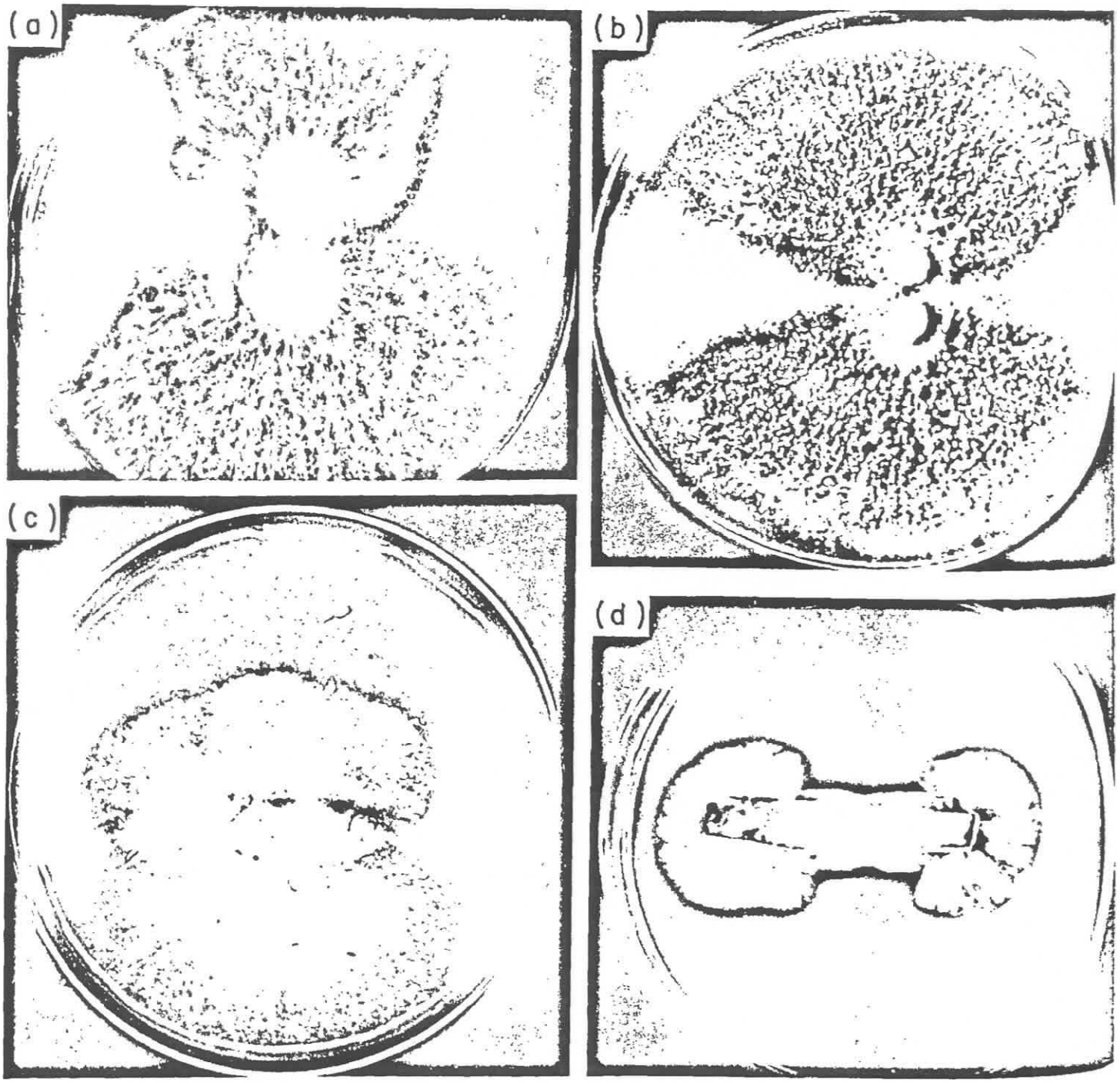

Fig. 3. Intraspecific interactions in culture between (a) mating type incompatible sib-related basidiospores of *Stereum hirsutum* showing the "bow tie" interaction (from Coates, Rayner and Todd, 1981); (b) a "bow-tie" like region occupied by white aerial mycelium between two sib-related single-ascopore cultures of *Daldinia concentrica*; (c development of a possibly heterokaryotic outgrowth (from the interaction zone between two somatically incompatible cultures of *Hypoxylon fuscum*. ((b) and (c) are reproduced with kind permission from P. R. Sharland); (d) outgrowth following subculture of a strip of agar plus mycelium from across the interaction zone between sib-related mono-ascospore isolates of *Hypoxylon serpens* (reproduced with kind permission from C. G. Dowson).

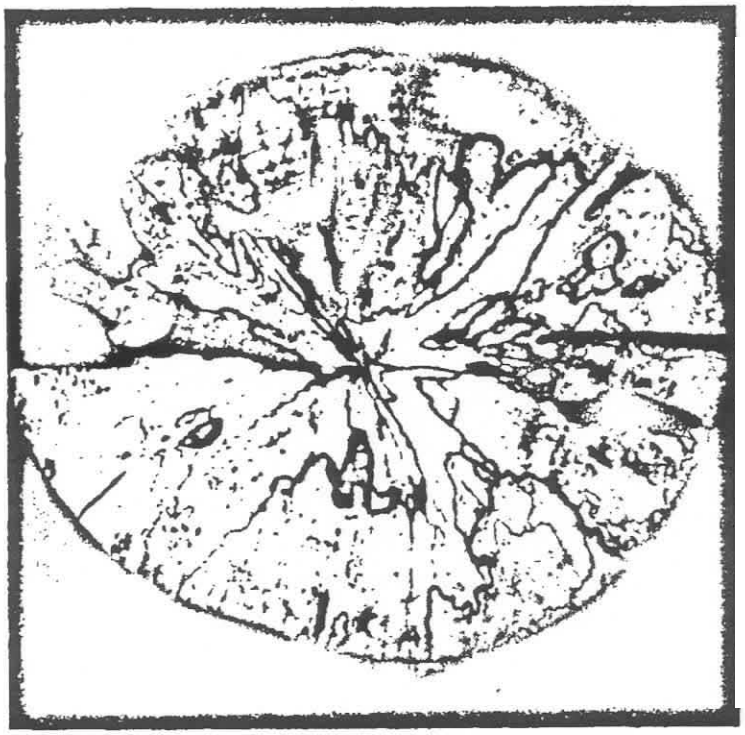

Fig. 4. Transverse section of a decaying beech (*Fagus sylvatica*) log showing interaction zone lines separating decay columns occupied by different fungal genotypes. (Reproduced with kind permission from I. Chapela.)

ous individuals, there may be reduction in size of sporophores, and even inhibition of overall activity in decay (Rayner *et al.*, 1984). Another important consequence is that individuals which are positionally advantaged, or become so as a result of faster extension rates, may come to occupy extensive volumes of wood ahead of their competitors.

However, somatic incompatibility need not always result in the clear demarcation of mutually exclusive individuals. In some cases this could occur because the individuals are so irretrievably intermixed that they cannot form discrete decay columns; for example, in beech logs inoculated with basidiospore suspensions of *Coriolus versicolor*, *Bjerkandera adusta* or *Stereum hirsutum*, the colonized wood became extensively discoloured, but not visibly decayed, and numerous genotypes were obtained by isolation from small samples (Coates, 1984). Alternatively, where the somatic rejection is partially or wholly non-persistent, as may occur in some of the xylariaceous fungi exhibiting access phenomena (see above), then clear demarcation between domains may not occur.

II. MODES OF ARRIVAL

A primary factor affecting population structure of decay fungi in living trees

is their manner of arrival at appropriate colonization courts. Essentially, arrival may be effected either by vegetative mycelium or by dispersed propagative units which may be either identical or dissimilar genetically. These modes of arrival are characterized by distinctive infection or colonization processes and by contrasting patterns of organization of the surrounding population.

A. Arrival by Mycelium

Arrival by mycelium is often important in root-infecting pathogens which are dependent either on root-contact, as with *Heterobasidion annosum* and non-rhizomorphic *Armillaria* spp., or on interstitial mycelium ramifying through soil and often organized into plectenchymatous cords or rhizomorphic organs, as with *Armillaria mellea*, *A. ostoyae* and *Rigidoporus lignosus*. Colonization via mycelium offers several potential advantages. These include the possibility for synergism between individual hyphae within the mycelium, the possibility for multiple infection foci for the same genotype, and subsequent coalescence between these, and the opportunity for import of nutrients and water from exogenous sources. All these result in the development of considerable inoculum potential, which in turn has been associated with the "ectotrophic" habit adopted by root pathogens (Garrett, 1970).

Also important is the fact that mycelial colonization provides an opportunity for the same genotype to spread from tree to tree. It can thus be no coincidence that several population studies of root pathogens have demonstrated, by somatic incompatibility testing or other means, the presence of the same genotype in adjacent trees. One of the first of these studies was with *Phellinus weirii* by Childs (1963) who found groups of Douglas fir (*Pseudotsuga menziesii*), often more than 50 m wide, infected by the same genotype.

Similar findings have been obtained with *Armillaria* species, where isolates of apparently the same genotype have commonly been obtained over 100 m apart, and as much as over 800 m apart (Adams, 1974; Shaw and Roth, 1976; Korhonen, 1978a; Anderson *et al.*, 1979; Thompson and Boddy, 1983). Unfortunately, because of the criteria chosen for identification of genotype, there is some difficulty of interpretation of these *Armillaria* studies. In some cases, the formation of a dark demarcation zone between colonies has been used (Adams, 1974; Shaw and Roth, 1976), but there is now evidence that such dark zones characterize pairings between sexually intersterile groups ("biological species") of *Armillaria*, whilst unpigmented demarcation zones often occur between different genotypes within the same sterility group (Ullrich and Anderson, 1978; Korhonen, 1978a). Other studies have used only mating-type alleles, it even being suggested that these provide the only definitive criterion (Anderson *et al.*, 1979). However, this cannot be so since

sib-composed secondary mycelia—that is, ones arising from matings between spores from the same fruit body—carry identical mating-type alleles even though being of manifestly different genetic origin.

Above all, these problems indicate the need in all population studies to characterize adequately the genetic systems resulting in mating and somatic incompatibility and in their interaction. Thus, in the case of *Armillaria* there is a clear requirement for a combination of mating-type and somatic incompatibility analysis, as demonstrated by Korhonen (1978) who identified individual genotypes of as much as 120–150 m in diameter in a Finnish forest stand and Kile (1983) who isolated the same genotype of *A. luteobubalina* over 500m apart. Incidentally, although groups of isolates of the same genotype have sometimes been referred to as clones, since physical discontinuity within the natural population cannot be established with certainty, it is possibly better to refer them to the same 'mycelial type' or genotype.

With respect to *Armillaria*, effort has sometimes been made to find another fungus suitable as a biological control agent in forest stands, as with *Phlebia gigantea* which is effective against *Heterobasidion annosum* (Rishbeth, 1963). In this connection the need to find an organism with a similar colonization strategy (i.e. one which competes for the same niche) is paramount, and several decay-causing Basidiomycotina which form mycelial cord systems ramifying through woodland litter have been suggested as possible agents (Rayner, 1977; Thompson, 1984). Population studies of some of these fungi have demonstrated the presence of widespread mycelial types, and in stands of suppressed trees co-occurrence and competition with *Armillaria* spp. has been shown (Thompson and Rayner, 1982; Thompson and Boddy, 1983; Fig. 5).

With respect to *Heterobasidion annosum* a somewhat different population structure may be expected, reflecting its different colonization strategy. The accepted model for spread of this fungus in conifer plantations is that airborne basidiospores germinate on cut stump surfaces giving rise to mycelia which penetrate to the roots and then spread to adjacent trees via root contact (Rishbeth, 1951a, 1951b). Since the fungus is outcrossing, with a unifactorial homogenic incompatibility system (Korhonen, 1978a), heterogeneity at the infection foci (i.e. stumps) is to be expected, but subsequent mycelial spread will give rise to the presence of the same genotype in different trees. Exactly this situation has been demonstrated in *Pinus resinosa* plantations in Vermont, USA, by Chase and Ullrich (1983).

B. Arrival by Propagules

Unlike mycelium, dispersal units—generally speaking, spores—have limited ability to import resources for colonization. They cannot, therefore, generally be expected to exert the same level of inoculum potential at a resource surface

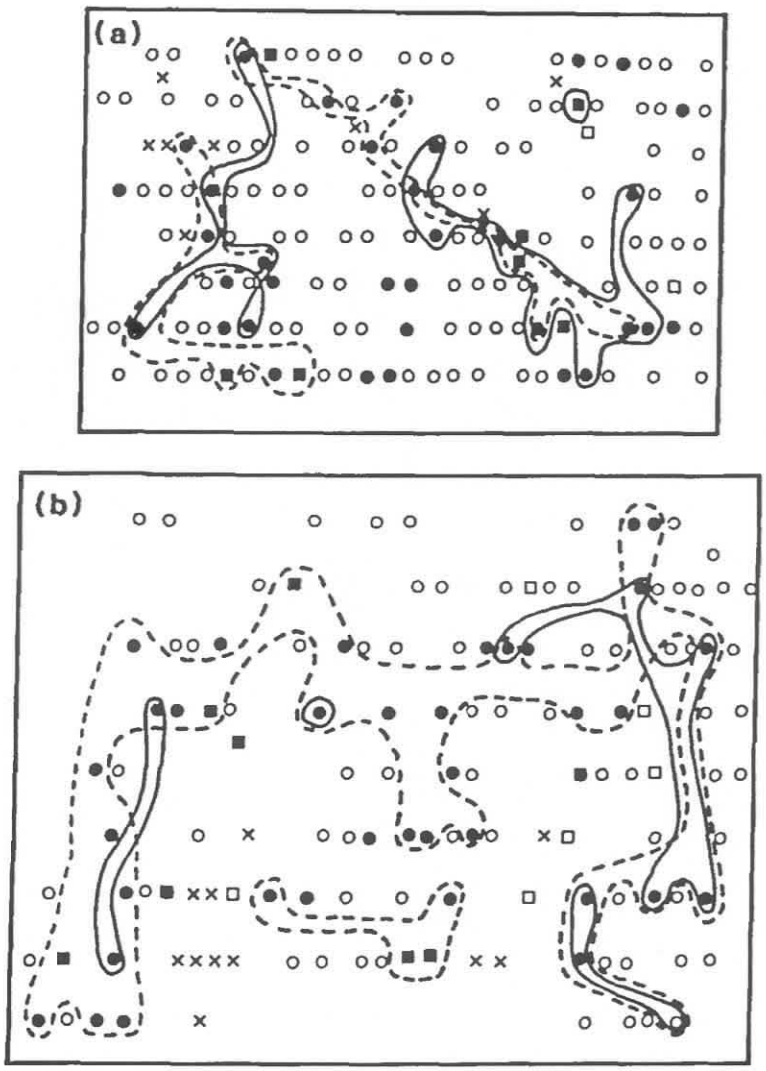

Fig. 5. Distribution of different mycelial types of *Phanerochaete velutina*, *A. bulbosa* and *A. ostoyae* in (a) 28 × 7 m site of p. 55 oak at Savernake and (b) 50 × 11 m site of p. 43 oak at Forest of Dean. ●, Sampled dead oaks; ○, living oak; ■, sampled stumps of fallen suppressed oaks; □, large oak stumps from trees grown previously on the site; X, trees other than oak; —, delimitation of trees/stumps colonized by the same mycelial type of *Phanerochaete velutina*; ----, delimitation of trees/stumps colonized by the same mycelial type of *A. ostoyae* at Savernake and *A. bulbosa* in the Forest of Dean. (From Thompson and Boddy, 1983.) Reprinted by permission from New Phytological Trust. Copyright © 1983.

although this barrier may be circumvented if introduced by a vector. Colonization will inevitably be from localized foci, and whilst the opportunity for synergistic coalescence between these is available, this depends on the propagules being genetically identical for somatic incompatibility factors.

1. Genetically Identical Propagules

In outcrossing populations the production of genetically identical propagules will be dependent on asexual (i.e. mitotic) devices, principally conidiogenesis. Whereas conidia are commonly abundantly produced by Ascomycotina,

including the wood-decaying Xylariaceae, they are less frequent in Basidiomycotina where they are in addition (but not necessarily) associated with the homokaryotic phase.

Unfortunately, except in a few specialized cases, the role of conidia as colonization units in decay fungi has not been established, and emphasis has mostly been placed on ascospores and basidiospores. However, one case where the role of conidia has been established concerns the arthrospores of *Amylostereum chailletii* and *A. areolatum* which are carried within intersegmental pouches and deposited during oviposition by certain wood wasps (Boidin and Lanquentin, 1984). Here, the vector plays a vital role in establishing its symbiotic associate below the wood surface obviating hostile micro-environmental conditions and thereby enhancing inoculum potential, presumably all the more so because the propagules are homogeneous. This is reminiscent of the situation in *Ceratocystis ulmi*, where the form of inoculum carried to the feeding grooves by the bark beetles may be all-important in the establishment of infection (Webber and Brasier, 1984; see also Brasier, this volume).

Another circumstance where the colonization potential of conidia has been demonstrated, at least artificially, concerns their use in establishing *Phlebia gigantea* at cut stump surfaces to control *Heterobasidion annosum* (see above). This presumably developed because of ease of artificial production of inoculum by this means. However, it is interesting to note that one additional advantage will be facilitated—colonization by a homogeneous inoculum—as compared with a heterogeneous basidiospore inoculum which might well prove less successful.

Whereas in outcrossing species, basidiospores and ascospores may be expected to be genetically heterogeneous, this will not apply in non-outcrossing forms which produce homokaryotic basidiocarps or ascocarps and clonal progeny. It will be apparent that this may have important consequences for the infection biology of such fungi, obviating the problems of somatic incompatibility and allowing synergism between infection foci.

2. *Genetically Different Propagules*

These include ascospores and basidiospores developed meiotically from initially heterokaryotic hyphal compartments, i.e. asci and basidia. Simultaneous infections will hence give rise to separate foci delimited by somatic incompatibility (following initial mating to form secondary mycelia in the case of basidiospores). Spatial competition for domain between mycelia developing from these foci will follow, and as already indicated, where the initial inoculum load is considerable may even lead to inhibition of further development and resource exploitation. Obviously, this type of situation can only occur where an infection court is sufficiently large and receptive to germination.

III. MODES OF ENTRANCE AND ESTABLISHMENT: INVASION STRATEGIES

A. Heartrots

A long-established view, originating from the studies of Hartig (1874, 1878), and supported until relatively recent times (Boyce, 1961; Peace, 1962), assumes that heartrot, decay of the dead central heartwood, represents the predominant decay type in standing trees. Underlying this view is the notion that saprotrophic growth is possible in the dead, aerated tissues, despite the high levels in some cases of allelopathic extractives, but not in the living, water-filled sapwood. Accordingly, early emphasis concerning the practical management of decay was placed on the elimination or prevention of infection courts (wounds, dead branches or roots) sufficiently large to expose the susceptible heartwood tissues; so long as the latter remained unexposed, the tree was held to be "safe" from decay other than by truly "parasitic" fungi.

More recently, it has become clear that these heartrot concepts are only partially true and that sapwood decay can develop in trees lacking a true heartwood (e.g. species of *Betula*, *Acer*), and as a result of sapwood injury, direct pathogenesis or predisposition by environmental stress or root-infection (see below). Furthermore, it is clear that the heartwood may be accessed via quite small infection courts including small branches and stubs, as with *Stereum gausapatum* in oak (Cartwright and Findlay, 1958; Toole, 1961; Boddy and Rayner, 1982), and even living branch stubs < 1 cm diam. as with *Echinodontium tinctorium* in western hemlock (Etheridge and Craig, 1976).

A generally important feature of heartrots is that if colonization foci are limited in space or time a considerable volume of resource may be made available to a limited number of colonists, so that an individuals' domain can become very considerable. This is presumably enhanced by selective effects of allelopathic extractives, and in addition will be influenced by the mode of entry of the fungi concerned. Here an initial dichotomy concerns whether the fungus invades through the roots or aerial portions of the tree, giving rise respectively to "butt rot" or "top rot" decay patterns.

1. Root Invasion: Butt Rots

As will already be apparent, invasion by butt-rot fungi may be expected often to occur following arrival of vegetative mycelium. In such cases the enhanced inoculum potential combined with possibilities for tree-to-tree spread will probably result in predominance in the decay of a single genotype which as it progresses up the trunk will come to command a considerable domain (cf. Fig. 6). This probably occurs with *Phellinus weirii* in Douglas fir (*Pseudotsuga*

menziesii), *Armillaria bulbosa* in mature deciduous trees (Rishbeth, 1982) and *Heterobasidion annosum* in conifers other than pine (on which it is an ectotrophic pathogen) such as larch (*Larix* spp.), spruce (*Picea* spp.) and Douglas fir (*P. menziesii*). However, here our choice of examples is limited by the lack of knowledge of arrival and invasion patterns in the vast majority of butt-rot fungi, and population studies of these are urgently required: *Grifola frondosa* and *Inonotus dryadeus* in *Quercus*, and *Meripilus giganteus* and *Ustulina deusta* in *Fagus* are just some examples where studies may be expected to be fruitful.

Where root-colonization is effected via a genetically diverse inoculum, then there should be a greater chance of concurrence of different individuals within the main stem, the position of each being correlated with the roots through which invasion initially occurred. However, as where different branches serve as infection courts in development of top rots (see below), multiple infections established in the outer part of a branching system will be progressively filtered out as they converge towards the centre where only a few, positionally advantaged individuals may be expected to predominate.

This type of effect, or sparsity of initial colonization foci, may account for the population structure of *Phaeolus schweinitzii* in Sitka spruce (*Picea sitchensis*) and Scots pine (*Pinus sylvestris*) plantations, where basidiospore infection from the soil has been implicated (Barrett and Uscuplic, 1971). Here it was found that isolates from different, even closely adjacent trees were invariably somatically incompatible, but isolates from different positions in the same tree intermingled freely in culture. Hence it appears that each tree contains a single, unique genotype and that there is no mycelial spread between trees, a situation which clearly indicates a genetically diverse inoculum such as would be provided by basidiospores. However, basidiospores in themselves cannot be expected to exert much inoculum potential of the type which is generally deemed necessary for root invasion (Garrett, 1970), so some means of obviating this requirement might be important. Of interest here is evidence that root-infection by *Armillaria* predisposes trees to infection by *P. schweinitzii*. The latter apparently colonizes infection foci of the former and readily replaces it in culture (D. K. Barrett, personal communication). This type of primary/secondary pathogen interaction raises fascinating possibilities with respect to the establishment of an infection base and may prove to be a more frequent factor in decay aetiology than is presently realized (see also below).

2. *Top Rots*

As already implied, the combination of genetically diverse basidiospore inoculum with large or multiple infection courts provides ample opportunity for concurrence of different genotypes of top-rot fungi within heartrot decay columns. Reports of multiple infections, indicated by somatic incompatibility between isolates obtained along the length of the trunk, are therefore to be

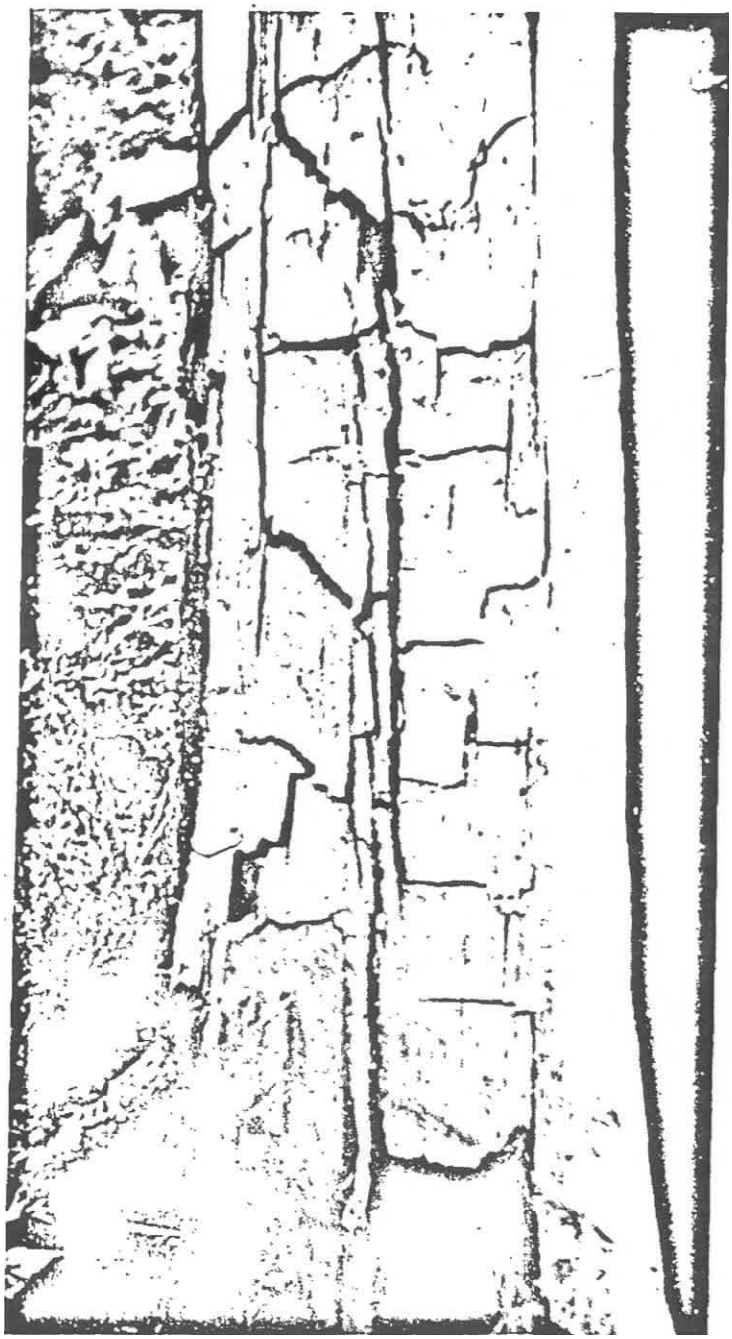

Fig. 6. "Butt rot" caused by *Phaeolus schweinitzii*.

expected and examples include *Phellinus pini* in Douglas fir (*Pseudostuga menziesii*) (Roth, 1952), *Fomitopsis cajanderi* also in Douglas fir (Adams and Roth, 1967, 1969), and *Ganoderma applanatum* and *Daedaleopsis confragosa* in deciduous trees (Scherer, 1973, cited by Esser and Meinhardt, 1984). However, in all but one of these cases the cultural work was not supported by studies of the mycelium in the wood itself. The exception was the study of Adams and Roth (1969) on three ice-damaged trunks infected by *F. cajanderi*, where somatically incompatible mycelial mats developed in juxtaposition at the surface of sections of trunks incubated in polythene for 5 months. Importantly, their results indicated a larger number of individual types near

the infection courts than further down the trunk. This is consistent with the expected reduction in numbers as positional primacy is exerted with progressive distance from the point of entry.

Multiple infection has also been demonstrated for the Indian paint fungus, *Echinodontium tinctorium*, but in this case is due to the numerous, separate, localized decay foci in heartwood which can be traced to the small branch stubs which are believed to provide avenues for infection. Importantly, the fungus can be isolated from apparently healthy twigs, substantiating the possibility that cryptic colonization ("latent invasion"—see below) of these could provide an infection base (Etheridge and Craig, 1976). However, the genetic analysis which could confirm this possibility does not appear yet to have been done.

A somewhat analogous situation occurs with *Stereum gausapatum*. Although this fungus has long been recognized as a cause of "pipe rot" in heartwood of *Quercus*, it is clear that it can gain access to the latter through branch stubs (Cartwright and Findlay, 1958). Furthermore, recent studies have demonstrated that it is a major colonizer of sapwood in living, or partially living, attached branches, where it frequently occurs as one or only a few individuals occupying considerable wood volumes (Boddy and Rayner, 1982; Fig. 7a; see also below). In these cases the sapwood may sometimes be extensively decayed without any overt colonization of the heartwood, but on other occasions decay in the heartwood can be genotypically correlated with that in adjacent sapwood (Fig. 7b). Clearly then, there is the potential for establishment of a substantial colonization base in sapwood, allowing invasion of the heartwood in branches whence the fungus gains direct access to the heartwood of adjacent trunks or more major branches. An interesting corollary of the ability of *S. gausapatum* to invade heartwood is the readiness by which it directly transgresses "heartwood wings". The latter have been described as zones of prematurely formed heartwood abutting the edges of decay columns in partially living branches (Boddy and Rayner, 1981). Direct transgression of these zones by *S. gausapatum* may result in several being formed in rapid succession (Fig. 7a). These delimit what appear to be separate decay columns, but that a single genotype is involved can readily be shown by somatic incompatibility testing.

B. Colonization of Disrupted Sapwood

Although the sapwood of living trees may generally be considered a selective and inhospitable habitat for fungi, due to its high moisture content, low available nutrient levels and possible responsiveness to infection, there are two major circumstances under which these stresses may be alleviated. The first is where sapwood function is disrupted by large-scale injuries or death or

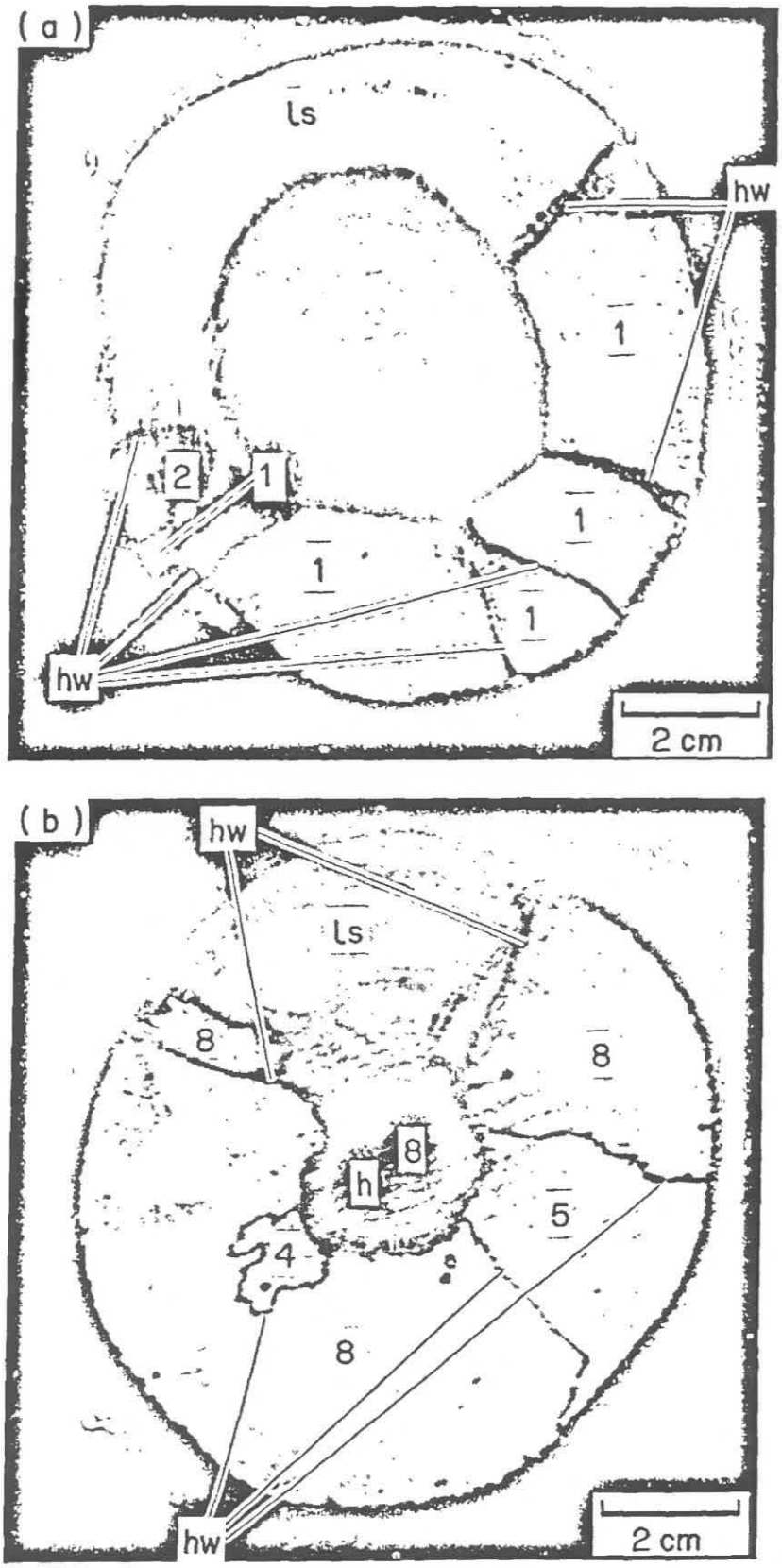

Fig. 7. Transverse sections through branches infected by *Stereum gausapatum* showing distribution of different individuals (code numbers 1, 2, 4, 5 and 8); heartwood (h), heartwood wings (hw), interaction zone lines (i) and living sapwood (ls). In (a) note successfully formed heartwood wings which have been transgressed by *S. gausapatum*. In (b) note that the same genotype of *S. gausapatum* was isolated from heartwood and adjacent sapwood. (From Boddy and Rayner, 1982.) Reprinted by permission from Transactions of the British Mycological Society. Copyright © 1982.

adjacent bark, exposing what may be a considerable volume of tissue to colonization. The second is where physiological stresses or damage resulting from direct pathogenesis by fungi results in an endogenous predisposition of intact tissue to colonization, via lowering of water content, increase of nutrient availability or loss of responsiveness to infection.

The effects of major wounds on colonization of standing trees by decay fungi have been extensively studied, commensurate with the proposition that such wounds provide the main if not sole source of decay (e.g. Shigo, 1966, 1967, 1979; Shigo and Marx, 1977; Mercer, 1982). Two important observations have regarded the localization of decay to tissues within the immediate vicinity or sphere of influence of the wounds and the invariable occurrence of non-decay organisms at early stages of colonization and at the periphery of decay/discoloration columns (Fig. 8). Although extensively interpreted in terms of interplay between active defence responses of living sapwood and invasiveness of microbial colonists, it has been pointed out that the patterns of localization and apparent "succession" from non-decay micro-organisms to decay fungi can be understood in relation to purely anatomical constraints, limited aeration, and expected changes in *dominance* from ruderal to combative organisms (Boddy and Rayner, 1981a; Cooke and Rayner, 1984). Thus similar patterns of colonization can be observed in freshly cut stumps, logs and even long-dead woody material placed under suitable conditions for colonization where an active host defence response is obviated. In all these cases the sequence of colonization is that expected according to a general model of community development pathways following enrichment disturbance, a process involving sudden exposure of a large volume of essentially virgin domain (Cooke and Rayner, 1984). Ruderal organisms, with life cycles characterized by rapid reproductive commitment and effective dispersal mechanisms are dominant initially, but become replaced by combative organisms K-selected for a longer individual life span.

Unfortunately, the extensive studies of colonization from major wounds in standing trees have mostly neglected intraspecific interactions between fungi, in favour of the supposed fungus–host interaction, and interspecific fungal interactions underlying the apparent successional events. However, the similarities just mentioned between colonization processes in wounded trunks and cut stumps and logs, where intraspecific interactions have been studied, allow the latter to be used as a model for probable events in standing trees.

Studies of cut hardwood stumps and logs (see Rayner, 1977, 1978; Rayner and Todd, 1979; Coates, 1984) have revealed different types of population structure of decay fungi corresponding to different colonization strategies. Several widespread actively white-rotting Basidiomycotina colonizing via airborne spores, such as *Bjerkandera adusta*, *Coriolus versicolor*, *Stereum hirsutum* and *Phlebia radiata* are characterized by coming to dominance after a moderate

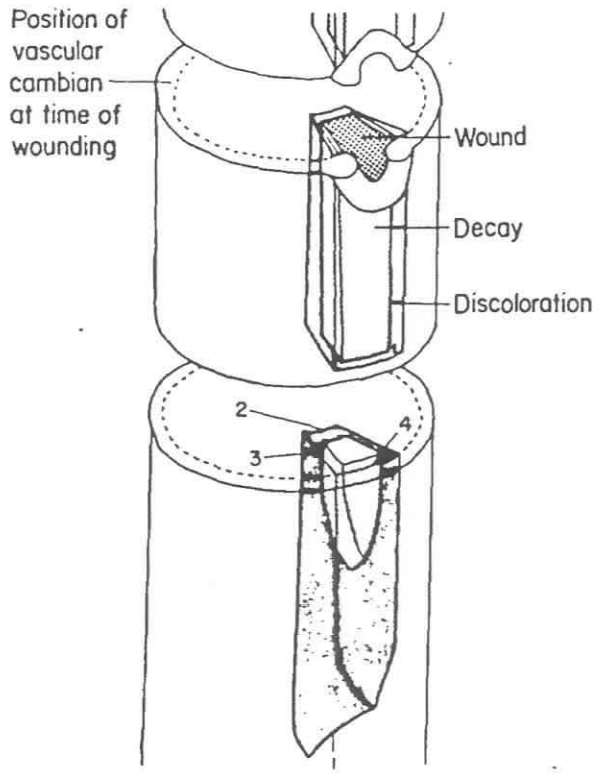

Fig. 8. Diagram illustrating localization of decay and discoloration in wounded sapwood of a living tree. The positions of the supposed compartmentalizing "walls" 1, 2, 3 and 4 (see Shigo and Marx, 1977) are shown. Scale bar represents 2 cm. (From Boddy and Rayner, 1983a.) Reprinted by permission from New Phytological Trust. Copyright © 1983.

time interval (often after 6–12 months or more) and producing clearly demarcated decay columns occupied by multiple genotypes within individual resource units. In untreated cut stumps remaining partially alive, their decay columns are markedly localized within the wood near the cut surface. However, *Phlebia radiata* is selectively favoured in cut stumps treated with the herbicide ammonium sulphamate (Rayner, 1977) and this corresponds with its usually late development in dead trunks and branches of standing trees (see below). *Stereum hirsutum* is also commonly found on standing trees, especially of oak, but here it is evidently selectively associated with cut or broken branch stubs where it produces multiple individuals in localized decay columns, and is absent from intact branches where *Stereum gausapatum* predominates. *S. gausapatum* may, however, also sometimes colonize cut or broken stubs, where numerous localized genotypes can be present, unlike in intact branches where, as is described elsewhere, one or a few genotypes occur. This is further emphasized by the results of recent experiments where *S. gausapatum* was deliberately inoculated into wounds in attached oak branches (Boddy and Rayner, 1984a). Limited decay columns were formed, corresponding with the localization expected within the vicinity of wounds (Fig. 9). However, the inoculated branches were simultaneously naturally colonized by other *S. gausapatum* genotypes forming extensive decay columns.

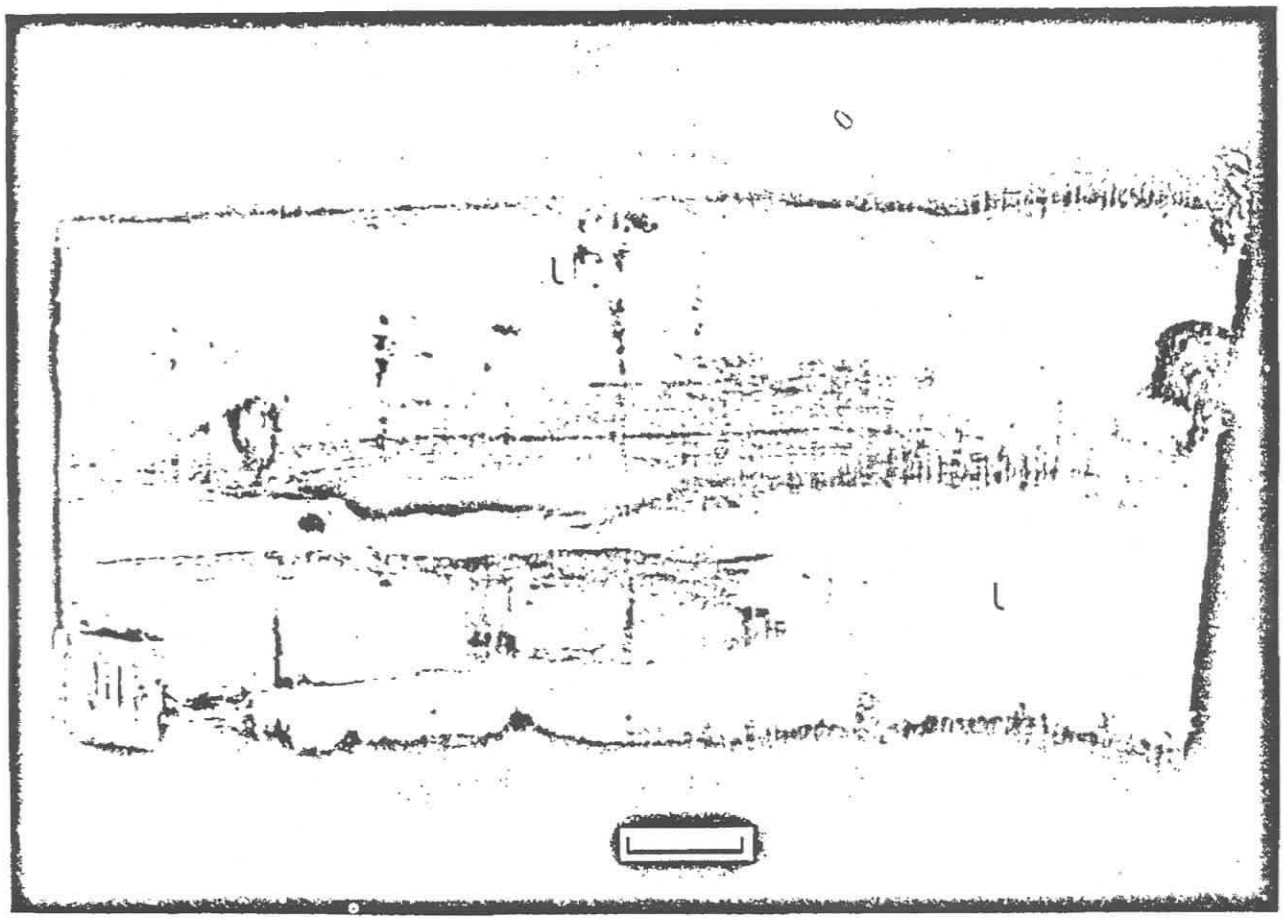

Fig. 9. TS through a branch, 47 weeks after inoculation with *Stereum gausapatum*, showing localization of decay: i, inoculum plug; l, living sapwood. Scale bar represents 1 cm.

Finally, it must also be said that *B. adusta*, *C. versicolor* and *S. hirsutum* can also sometimes be found in intact trunks and branches, perhaps especially as a result of predisposition by drought or disease (see below), whence they in turn typically form extensive, single genotypes. *C. versicolor* has indeed sometimes even been implicated as a pathogen, notably in apple (*Malus* spp.) (e.g. Thomas, Mathee and Hadlow, 1978). These observations clearly establish the different population patterns associated with colonization of a large, suddenly exposed colonization court, and those in intact trees or branches.

The Ascomycotina species *Xylaria hypoxylon* has a somewhat similar colonization strategy to the Basidiomycotina just mentioned, in that it regularly produces numerous clearly demarcated decay columns occupied by different genotypes. However, it is less active in decay, and the decay columns become discernible very rapidly, often being distinct within 3–6 months. It is rarely found in standing trees, although it sometimes produces complex mosaics of genotypes on decorticated trunks and branches of sycamore (*Acer pseudoplatanus*). Here the shape of the occupied zones is irregular and not in the form of columns, colonization being effected from the cambial zone.

The airborne Basidiomycotina *Chondrostereum purpureum*, *Corticium evolvens*,

Flammulina velutipes and probably *Schizophyllum commune* possess ruderal characteristics in that they predominate and produce fruit-bodies at early stages of community development, but cause little decay and are readily replaced by the more combative, active decay fungi. *Chondrostereum purpureum* is of particular interest because of its pathogenicity in a variety of fruit trees where it causes silver leaf disease. It is also an almost ubiquitous early colonizer of cut hardwood stumps, logs, brashing, etc. (but it is rarely found on oak where its niche is probably taken by *Stereum hirsutum*). Inoculation studies have demonstrated its remarkable capacity for rapid extension into wounded sapwood, at a rate far greater than that of more active decay species (Rayner, 1979; Woodgate-Jones, 1982), and it seems unusually well-adapted to tolerate the adverse micro-environmental conditions. Perhaps this may be associated with tolerance of low oxygen tension, and ability to aerate the tissues it colonizes, together with its pathogenicity towards living cells which may result in nutrient release. There appears to be little definite published information about its population structure, and this is urgently required. In one study of colonization of cut beech logs, the fungus was found to establish sparsely but rapidly within a large volume of wood, and isolates from the same log were somatically compatible, suggesting that they belonged to the same genotype (Coates, 1984). This pattern of colonization would be explained if colonization was effected by latent invasion (see below) or by a homogeneous basidiospore source, as would be the case if fruit-bodies of the fungus were homokaryotic. However, Boidin (1971) has indicated that the fungus is heteromictic and possesses tetrapolar incompatibility.

Stereum sanguinolentum appears to exhibit a rather similar colonization strategy on conifers to that of *C. purpureum* on hardwoods, although it lacks the rapid rate of mycelial extension of the latter. Thus it is abundant on cut stumps, logs and brashing, and also regularly colonizes pruning woods as a primary invader (Cartwright and Findlay, 1958; Kaarik, 1974). In some localities it is regarded as a serious pathogen, and it certainly reduces the quality of much commercial timber. Here, population studies have recently been undertaken, whence it has emerged that British and Scandinavian strains of the fungus are reproductively non-outcrossing, producing homokaryotic fruit-bodies yielding homogeneous, somatically compatible progeny sets (Rayner and Turton, 1982; Rayner *et al.*, 1984; A. M. Ainsworth, unpublished). Different genetic lines do exist within the population, however, and these exhibit somatic incompatibility when interpaired. Hence the fungus is divided into numerous somatically incompatible clonal or near-clonal subpopulations in a manner remarkably similar to that found in the USA for the dandelion, *Taraxacum officinale*, with some clones being widely represented in different geographical locations, and others (about 60%) being restricted to

particular locations (A. M. Ainsworth, unpublished; Lyman and Ellstrand, 1984).

Death of bark can have variable effects on development of decay. In some cases, effects may be localized, so that only a peripheral layer—sometimes only the outermost annual ring—becomes colonized. On other occasions wedge-shaped zones or even the entire wood cylinder may be made accessible. The differences between these three situations is probably related to the water content of the wood and the degree to which bark death leads to drying. Optimal conditions for decay development are probably those in which wedge-shaped zones are formed, such that there is sufficient aeration for establishment of decay, but nonetheless maintenance of a supply of moisture preventing desiccation.

The upper parts of timbers of Elm (*Ulmus* spp.) trees suffering from Dutch elm disease provide an example where extensive, rapid death and decortication quickly result in desiccating conditions and inhibition of decay. Under these circumstances certain fungi, notably *Rhodotus palmatus*, appear to be selectively favoured, and this may be related to the readiness with which the mycelium produces chlamydospores (Gibbs and Gulliver, 1977; Rayner, Watling and Frankland, 1985). Less severe conditions obtain towards the base of the trees, where *Pleurotus cornucopiae* frequently establishes, possibly in part via mycelial colonization. This relatively combative species produces luxuriant mycelium and appears to compete successfully with *Armillaria*, a feature which may prove of significance in reducing invasion potential of the latter in woods and hedgerows containing dead elms (Rayner and Hedges, 1982). Incidentally, from a limited population survey, there is evidence of overlap of mating-factor alleles between samples of *P. cornucopiae*, a feature which is to be expected in a suddenly expanding population such as would have occurred following the elm disease epidemic (Coates, 1984).

C. Colonization of Intact Sapwood

Contrasting with patterns of establishment following the enrichment disturbance resulting from wounding or bark death are those where essentially intact sapwood, imposing all those selective conditions alluded to previously (p. 135), becomes decayed. Here the expected pattern of community development follows that where initiation is under high stress conditions whence, because of the limitation on opportunities for colonization, fewer individuals of fewer species begin the process (Cooke and Rayner, 1984). The ability to colonize under such circumstances will depend either on pathogenic mechanisms allowing breaching of physico-chemical barriers, or a latent invasion strategy allowing endogenous development. In practice, however, it is sometimes difficult to distinguish both between these two possibilities, and between

these and establishment from major colonization courts such as wounds (for example with *Stereum gausapatum*). Indeed any particular fungus may under different circumstances employ all three mechanisms. Further population studies may help resolve these difficulties in the future, and our assignment of certain fungi to a role in colonization of intact sapwood *per se* below, is necessarily somewhat tentative.

1. Colonization via Direct Pathogenesis

There are still relatively few examples where pathogenicity is ascribed a direct role in the establishment of decay fungi in standing trees. Even where it is, then a distinction has to be made between "wound pathogens", such as *Chondrostereum purpureum*, and those fungi where pathogenicity governs entry to intact sapwood. Some of the root-infecting pathogens, notably *Armillaria* spp. and *Heterobasidion annosum* on pines, undoubtedly fall into the latter category, but for several aerially invading fungi, the exact mechanism of establishment is much less certain.

With respect to *Armillaria* and *H. annosum*, infection is dependent on production of ectotrophic mycelium which, as mentioned previously, is in turn associated with arrival at the root surface as vegetative mycelium. The predominance of one or a few genotypes in the infected wood is thus to be expected solely as a consequence of the pattern of arrival and establishment.

By contrast, establishment in aerial portions of the tree cannot be effected by mycelium, and so the numbers of genotypes present will be affected by whether or not the colonizing propagules are genetically heterogeneous, and by the frequency with which they gain entry. Where meiospores of heteromictic species are the infective agents, and numerous infection sites occur, then the result will be development of a mosaic of individual genotypes in the infected wood.

The occurrence of numerous infection sites might be expected to be unusual within the context of the selective conditions governing entry into intact sapwood mentioned previously. However, one mechanism whereby this condition would be met is where the bark itself provides a reservoir from which infections can be established. Bark represents a heterogeneous intermixture of dead and living tissue, characterized by highly stressful micro-environmental conditions, but in which some limited saprotrophic existence may be possible. This allows latent infections to establish, with the fungi responsible only becoming active—and hence in many cases pathogenic—when the micro-environmental stresses present in the bark are alleviated, as when the tree itself becomes physiologically stressed, for example by drought. Numerous examples of canker diseases have been shown to be conditioned by stress to the tree (e.g. Bier, 1959, 1961). Furthermore, there is strong evidence in elm bark that mosaics of genotypes of *Phomopsis oblonga* develop in elm bark

via a latent invasion mechanism (Brayford, 1983; Webber and Gibbs, 1984). *Colpoma quercina* which infects oak (*Quercus*) twigs probably also establishes in this way, although it is not clear whether it truly causes decay (Boddy and Rayner, 1984b).

Oudemansiella mucida is, however, an undoubted decay species and is a highly selective colonizer of attached beech (*Fagus sylvatica*) branches in which it causes white rot. Numerous genotypes of this fungus can be found in the decaying branches (Fig. 10) where we have obtained preliminary evidence that its presence is strongly correlated with localized regions of bark necrosis (L. Boddy and A. D. M. Rayner, unpublished). There is thus the possibility that this fungus establishes a latent invasion in beech bark, becoming pathogenic when the tree or branch is stressed, and then in turn invading the wood as a mosaic of genotypes. *Oudemansiella radicata* may well exhibit a similar colonization strategy on beech roots (Campbell, 1938; A. D. M. Rayner, unpublished observations).

Fig. 10. Section of a branch, 12 cm diam., decayed by many different genotypes of *Oudemansiella mucida*.

Various canker-causing species of *Hypoxylon*, including *H. mammatum* on aspen (*Populus tremula*), *H. mediterraneum* on oak (*Quercus*) and *H. tinctor* on maple (*Acer*) also presumably gain access to the wood cylinder via bark necrosis. Interestingly, *H. mammatum* cankers, which result in economically

very serious losses, are associated with galls caused by the insect *Saperda inornata* (Anderson, Ostry and Anderson, 1976).

Contrasting with the situation where localized latent invasion and pathogenesis of bark may provide infection routes for access to the sapwood, is the behaviour which has been described for other canker-forming fungi. These "punk-rot" fungi, as they have sometimes been termed, appear to establish as heartrots or wound pathogens within the wood cylinder itself. Thus imprisoned, their only means of *exit* to produce sporophores or other structures is via the living cambial tissues, which they invade destructively, often producing a thick pad of mycelium which locally prises the bark free and may rupture it completely.

One example is *Inonotus obliquus*, the birch conk, whose production of tumourescent sterile conks on *Betula* contrast with its reputation as an anti-cancer agent in the USSR (Gammerman, Shupinskaya and Yatsenko-Kamelevski, 1963; Reid, 1976).

Several fungi, apparently invading intact sapwood, characteristically produce one or a few individually extensive genotypes in an infected trunk or branch. These include *Stereum gausapatum*, *Peniophora quercina*, *Phlebia rufa* and *Vuilleminia comedens*, all of which occur as pioneer white-rotting invaders of attached oak branches (Boddy and Rayner, 1982, 1983b, 1983c; Fig. 11). In some cases, notably with *Phlebia rufa*, colonization by these fungi appears to be promoted by light-suppression, but in others apparently sound branches on the outside of the canopy become invaded, and the question arises as to whether the fungi at least initiate colonization by direct pathogenesis. Inoculation experiments indicate that this may indeed be so for *P. quercina*, which tends to be limited to distal portions of branches, but more particularly for *V. comedens* and *S. gausapatum* which often invade the main body of the branch. All these fungi readily established decay columns from inoculation points and this was partly associated with necrosis of the surrounding cambial zone (Boddy and Rayner, 1984a; Fig. 9). However, these inoculation experiments whilst establishing the pathogenic potential of these fungi also indicated that their establishment in branches is not the consequence of direct mycelial spread from an infection court. This was because of the localization of decay columns arising following inoculation, compared with the extensive columns produced naturally (see also above).

Another fungus whose infection biology has been persistently enigmatic is *Piptoporus betulinus*, the birch polypore. The widespread selective occurrence of this fungus on moribund birch trees has always attracted speculation that this is due to its pathogenicity on *Betula* spp. However, the cause–consequence issue as to whether the trees are moribund because they are colonized by *P. betulinus* or *vice versa* has never been satisfactorily ascertained. Inoculation experiments, aimed at resolving the issue, have only confused it. Whereas

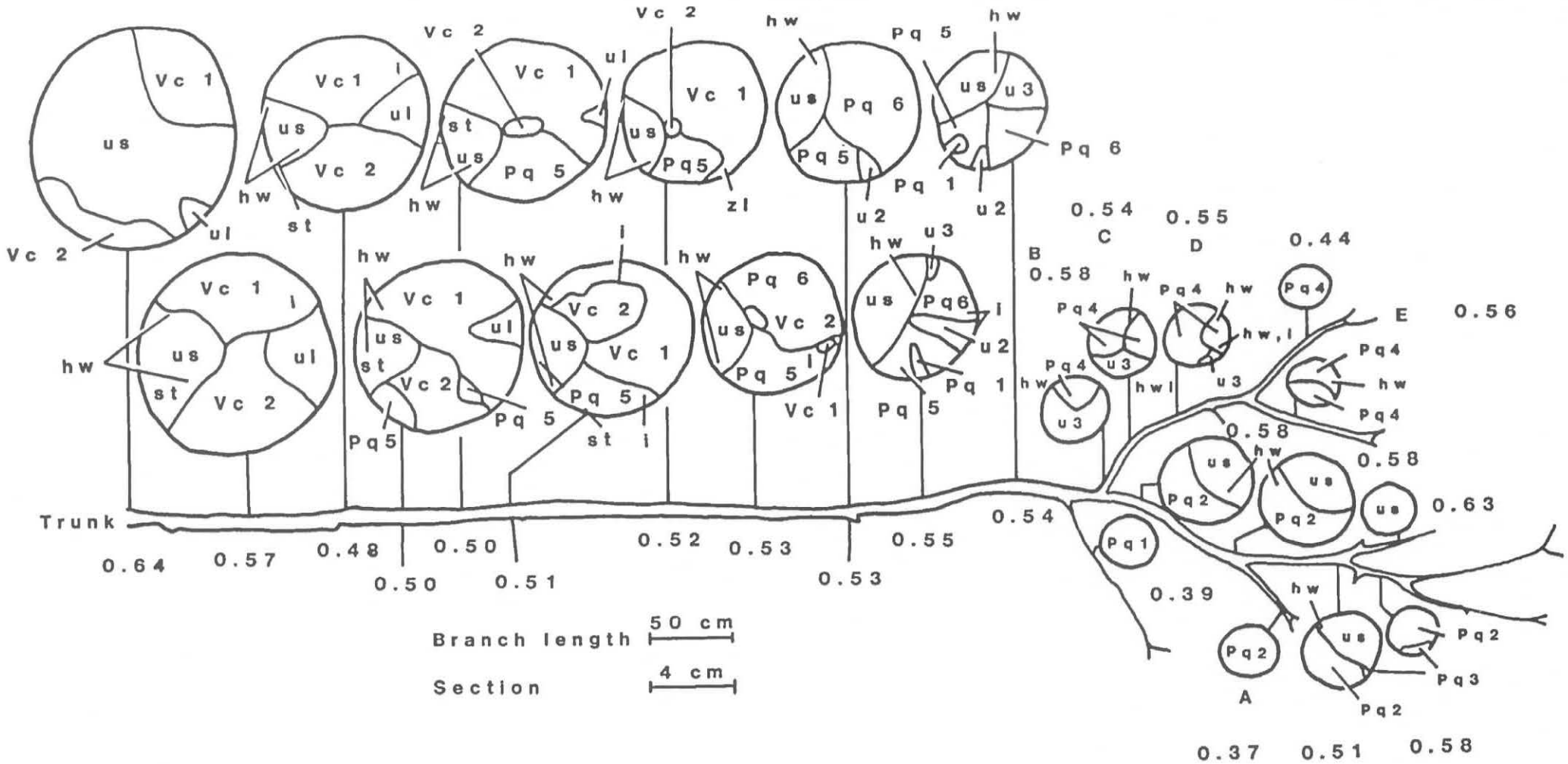

Fig. 11. Decay community structure in an attached oak branch. Different basidiomycete individuals were demarcated by interactive zone lines (1) in the wood. The predominant species were *Vuilleminia comedens (two individuals: Vc 1 and 2) and Peniophora quercina* (six individuals: Pq 1–6). Three other unidentified basidiomycetes (u 1–3) occupied relatively smaller volumes. Both *V. comedens* and one of the *P. quercina* individuals occurred in the main stem possibly originating from small branch stubs, or by direct entry. It is likely that Pq 2 originated in the branchlet from which section A was taken and progressed to the main fork whence it grew in both available directions. In the distal sections B–E, heartwood wings (hw) were present in the absence of living tissue (us) and separated decay columns occupied by either the same, or two different individuals. In the latter case, an interactive zone line was also present. Presumably the fungi were initially confined to regions between the heartwood wings, with living tissue outside. Subsequently, possibly following some traumatic event, the fungi were able, by some means, to penetrate or by-pass the wings, gaining access to the living wood and colonizing it without further wing formation. Values are given for relative density (g cm^{-3}). (From Boddy and Rayner, 1983c.) Reprinted by permission from New Phytological Trust. Copyright © 1983.

direct inoculations into healthy birch trees have met with limited success, the fungus can readily be cultured both on agar media and in wood blocks from a wide variety of trees (Macdonald, 1973; Cartwright and Findlay, 1958; Michaelopoulos-Skarmoutsis, 1980; Adams, 1982). Similarly, whilst some field surveys have been taken to show that the fungus is a serious pathogen (Vanin, 1922) others have led to the conclusion that it is unimportant, occurring only on weakened trees (Adams, 1982).

Population studies obviously have a place here. At one level these may set out to establish whether or not there is any correlation between pathogenicity and particular variants of *P. betulinus*, such as occurs between the sub-populations of *Ceratocystis ulmi* (Brasier, this volume). Here it may be significant that mycelial isolates of *P. betulinus* from Scandinavia and Britain are completely intersterile, associated with significant differences in cultural morphology and behaviour in spite of the close similarity between the respective basidiocarps (Burnett, 1975; Adams, 1982).

At another level, the population structure of *P. betulinus* in individual infected trees can be analysed to try to identify possible infection courts and modes of establishment. Such a study has recently been made (Adams, Todd and Rayner, 1981; Adams, 1982). Unfortunately, this study met with no success in trying to establish the infection courts from which *P. betulinus* colonized, being particularly limited by the rapid loss of tensile strength brought about by this brown-rot species, which rapidly leads to snapping of infected trunks and branches. Studies of birch trees with intact canopies failed to reveal *P. betulinus* even in attached twigs: the latter were suspected to harbour latent infections of *P. betulinus*, but only other fungi were isolated from them.

Examination of the distribution of individual genotypes of *P. betulinus* in infected birch trunks did, however, reveal some important patterns. Firstly, in no case was the same genotype obtained from more than one tree; this probably rules out the possibility of root-infection by mycelial spread and establishes basidiospores as the likely infective agents. Secondly, there was a significant difference between the number of genotypes found in trunks which were wind-thrown from the base associated with infection by *Armillaria*, and standing trunks or their attached branches. Out of the twenty-five trees which were sampled, the only ones containing more than two genotypes were those infected with *Armillaria*; one of these contained at least nineteen distinct dikaryons within a 1 m section of trunk (Fig. 12). Another three contained at least ten dikaryons over a similar distance.

These observations imply that in standing trunks, opportunities for infection are strictly limited, allowing rapid and extensive establishment of a limited number of genotypes, probably under predisposing conditions which have localized effects such as drought or light suppression. By contrast, root-

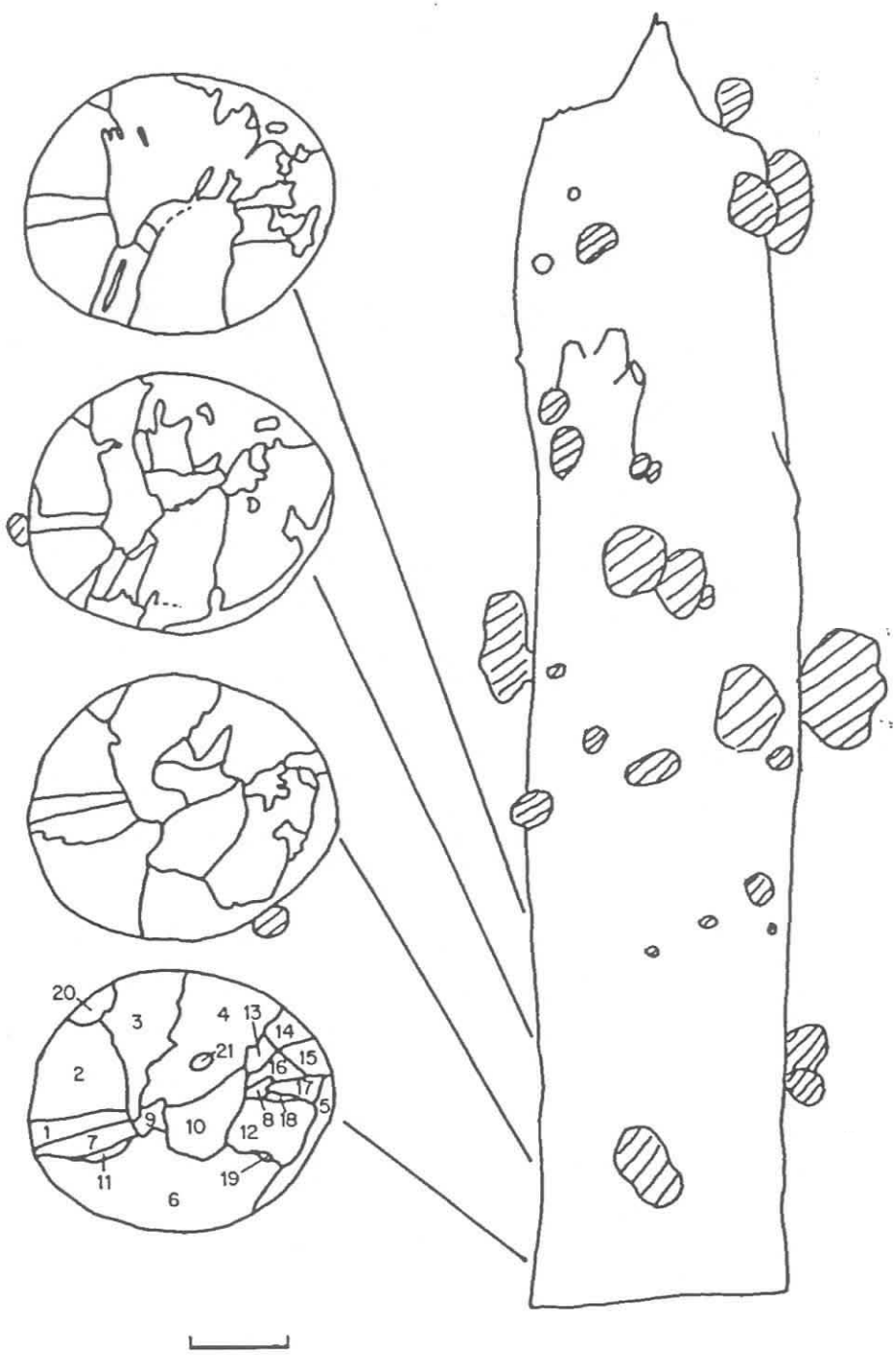

Fig. 12. Diagram of the upper part of a fallen birch (*Betula* sp.) trunk, the roots of which were colonized by *Armillaria* sp., illustrating numerous decay columns of *Piptoporus betulinus*. Figures represent different genotypes; hatched areas indicate positions of basidiocarps; scale bar represents 10 cm. (Reproduced with kind permission from T. J. H. Adams.)

infection predisposes the whole tree to multiple infections by *P. betulinus* whilst still allowing maintenance of sufficiently hostile micro-environmental conditions to exclude saprotrophic competitors. Some backing for this view came from a limited survey of a fire damaged stand. One of the six trees examined contained four dikaryons, and this larger number than normal might be attributable to the similar predisposing effects of fire damage and root-infection.

2. Predisposition and Latent Invasion Strategies

Discussion of such putative pathogens as *Stereum gausapatum* and *Piptoporus betulinus* should have established the principle that colonization of intact sapwood by decay fungi need not necessarily follow the convention of mycelial spread from a determinate infection court. In these, and many other decay fungi attacking standing trees, the extensive volume occupied by individual genotypes appears to be inconsistent with their measured rates of mycelial extension in culture. This is particularly reinforced by examples where decay columns occupied by a single genotype in excess of several metres long appear, on the basis of lack of additional annual rings in abutting living sapwood, to have developed within a single growing season (Figs 7 and 12). Such evidence has been found in attached oak branches colonized by *Stereum gausapatum*, *Phlebia rufa*, *Vuilleminia comedens* and *Peniophora quercina*, and although the cultural extension rates of these fungi may not be apposite to the natural situation, their rates of spread from deliberate inoculation were, if anything, even slower. It has therefore been suggested that these fungi establish decay from latent invasion of the intact, water-filled sapwood. Here they develop sparsely, and perhaps as propagules which become widely dispersed by the sap stream, reverting to active mycelial development as soon as the hostile micro-environmental conditions are alleviated by their own pathogenicity or by preconditioning external environmental constraints affecting the tree. A variety of xylariaceous Ascomycotina also seem likely to employ latent invasion strategies, as evidenced by their selectivity for particular tree species and rapid appearance on stressed trunks and branches.

One such fungus is *Daldinia concentrica* whose enigmatic behaviour has, albeit to a lesser extent, aroused the same controversy about its possible pathogenicity as *Piptoporus betulinus*. Population studies of this fungus have been initiated recently (P. R. Sharland and A. D. M. Rayner, in preparation; Boddy, Gibbon and Grundy, 1985) and reveal that it does indeed seem to exhibit several features in common with *P. betulinus*. Thus it is highly host-selective, being a more or less ubiquitous colonizer of moribund ash *Fraxinus excelsior*) trunks and branches; however, unlike *P. betulinus* it is *selective* rather than *specific* as it does occur on other tree species (Whalley and Watling, 1980, 1984).

Different genotypes of the fungus, including single ascospore isolates from the same perithecium appear virtually invariably to exhibit an obvious antagonistic mycelial interaction in culture (Fig. 3). Isolates from different trees invariably showed antagonism, establishing ascospores as the probable infective agents. Furthermore, isolations made from individual branch or trunk sections often revealed the presence only of one or a few genotypes. However, that this may not always apply was revealed by an extensive analysis of genotype distribution in a single, wholly dead wind-thrown trunk

over 13 m long whose roots were partially decayed by *Armillaria*. A total of thirty genotypes were found. Some of these were individually extensive occupying up to 4 m longitudinally and 50% or more of the cross-sectional area in the upper and lower portions of the trunk. However, others were inextensive and in the middle region of the trunk fourteen genotypes were detected within a single cross-section. There was some evidence also, that the trunk had been colonized in at least two stages, once some years before, and the other immediately following its ultimate death. The parallel with *P. betulinus* (see above) is striking, and reinforces the possibility that predisposition as a result of root-infection by *Armillaria* has very different consequences for population structure from other predisposing agencies such as drought.

With respect to drought, a variety of other Xylariaceous Ascomycotina, notably host-selective species of *Hypoxylon* appear to develop rapidly, that is within one or two years, following a hot dry season (Lonsdale, 1983). In some cases, as with *H. nummularium* on beech, these may produce extensive stromata or strip cankers many metres long and it hence seems highly probable that they are acting as latent invaders which establish decay as soon as micro-environmental stress in the sapwood is alleviated by drought stress of the tree. Further circumstantial evidence for this possibility is provided by the co-existence in drought-stressed beech branches of *H. nummularium* and the Basidiomycotina species, *Bjerkandera adusta* (Fig. 13). Individual genotypes of these species would normally be expected to be demarcated from one another, but evidence of their co-existence within the same domain has been found, and indicates that they may become intermixed as a result of possessing a common latent invasion strategy.

IV. THE PROBLEM OF SELECTIVITY: ADAPTATION AND ECODIFFERENTIATION

A. Occurrence and Possible Causes of Selectivity

As may already be apparent, considerable variability exists amongst tree decay fungi with respect to the extent to which they show selectivity or even specificity for particular trees. Thus *Piptoporus betulinus* (see above) appears to be completely specific to *Betula*, whereas the similar, but rare, species *P. pseudo-betulinus* occurs on aspen (*Populus tremula*), and another rare species, *P. quercinus*, occurs on oak (*Quercus*). Other examples of possible specificity are provided by *Oudemansiella mucida*, *Hypoxylon fragiforme* and *H. nummularium on Fagus*, and *Lyophyllum ulmarium* on *Ulmus*.

Strong selectivity for particular trees is exhibited, for example, by *Daldinia concentrica* and *Inonotus hispidus* on *Fraxinus*, by *Inonotus dryadeus* and *Stereum*

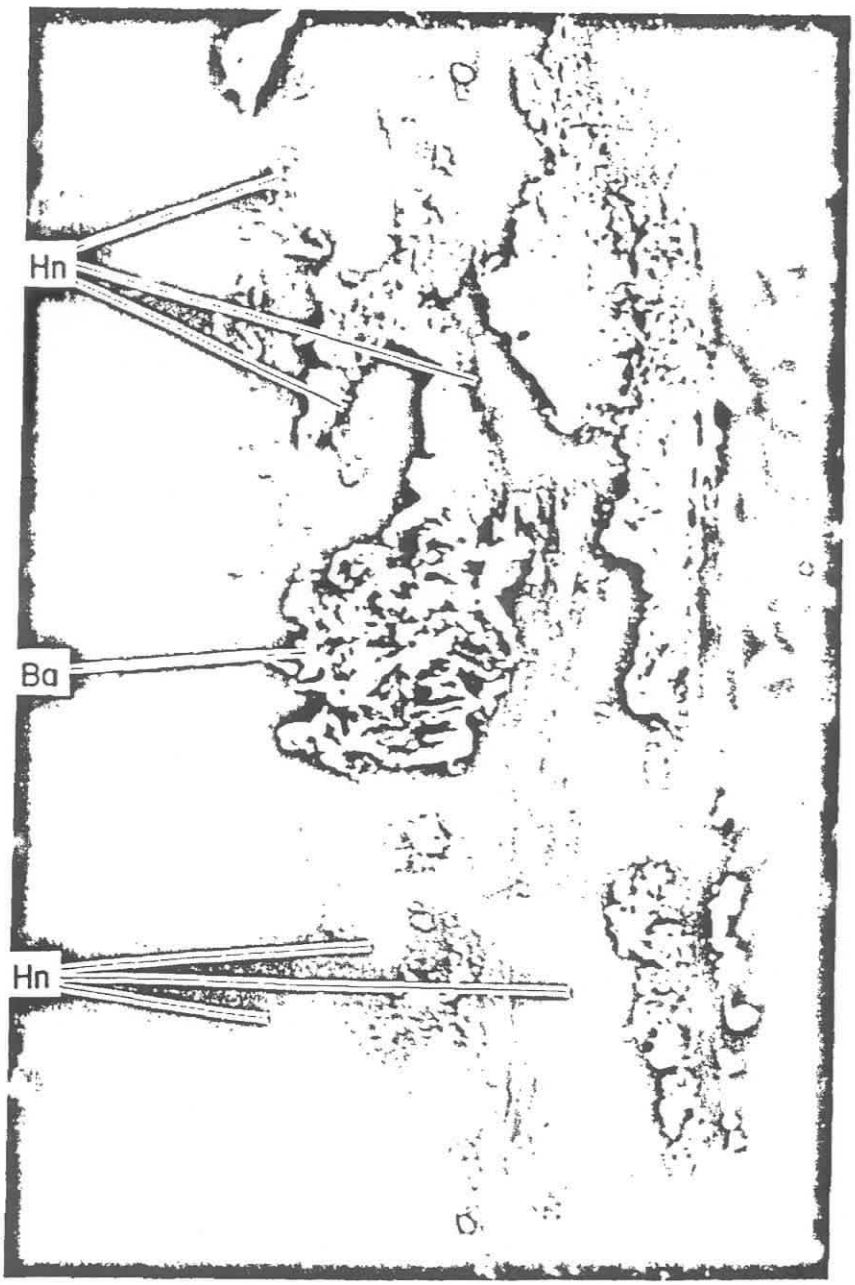

Fig. 13. Co-occurrence of fruit-bodies of *Bjerkandera adusta* and *Hypoxylon nummularium* on a section of beech (*Fagus sylvatica*) stem. Isolation and direct incubation revealed co-existence of these two species within the wood.

gausapatum on *Quercus*, and by *Fomes fomentarius* on *Betula*. Here the associations are not specific in that the fungi can be found on other trees, and in some cases there may be changes in selectivity with geographical location; for example in Britain *D. concentrica* becomes more frequent on *Betula* northwards, whereas *F. fomentarius* occurs on *Fagus* and *Acer* in the south.

A rather different situation occurs with fungi which, within the same geographical location, are selective for several, often taxonomically diverse, trees. A good example is *Laetiporus sulphureus* on *Quercus* (oak), *Salix* (willow), *Prunus* (cherry), *Castanea* (sweet-chestnut) and *Taxus* (yew).

Finally, some fungi exhibit non-selectivity, occurring on a wide range of host trees. In a few cases this range may include both coniferous and deciduous trees, but this situation is relatively unusual and even when it occurs there is marked selectivity for one or other type: thus *Heterobasidion annosum* which occurs widely on coniferous trees can also attack *Betula* spp.; by contrast *Pholiota squarrosa* which causes heartrot in a wide range of deciduous trees can occasionally be found on conifers. *Chondrostereum purpureum* and *Stereum sanguinolentum* have already been mentioned as wide-ranging colonists of deciduous and coniferous trees respectively, whilst *Vuilleminia comedens*, previously mentioned as a cause of decay in *Quercus*, also causes decay in attached branches of several other deciduous trees.

Such variations in host specificity and selectivity obviously demand explanation. The facile conclusion is that they represent varying degrees of adaptation towards particular hosts, but this then only raises the question of what such adaptation entails. Plant pathologists generally understand variations in specificity of plant pathogens directly in terms of the interaction between the virulence of the pathogen and resistance of the host. Unspecialized pathogens, with wide host ranges, such as *Botrytis cinerea*, invade when active resistance or passive non-susceptibility mechanisms are minimized, notably in juvenile, damaged or senescent tissues. However, in the case of specialized pathogens, host and pathogen alternately impose strong selection pressures for the development respectively of resistance and virulence in each other's populations. This sets the scene for complex sequences of co-evolution. These culminate in highly specific race-variety interactions conditioned by recognition or non-recognition of single genes resulting in compatibility (susceptibility) or incompatibility (resistance) in a manner remarkably reminiscent of the interaction between sexual compatibility and somatic incompatibility in Basidiomycotina mentioned above (Bushnell and Rowell, 1981; Heath, 1981; Ouchi, 1983; Tepper and Anderson, 1984; Rayner *et al.*, 1984).

One approach to the problem of selectivity of decay fungi in standing trees might therefore follow similar lines, that is in terms of the outcome of resistance/virulence-mediated direct interactions between the fungus and tree. This would be consistent with recent emphasis on responsiveness to infection as a major determinant of colonization potential, even (albeit with unconvincing evidence) in heartwood (Shigo and Marx, 1977; Shortle and Cowling, 1978; Shigo and Shortle, 1979). However, we believe such an approach would be erroneous for many tree decay fungi, for the following reasons: their essentially saprotrophic nutrition; lack of clear evidence for pathogenicity as a general determinant of colonization; often limited or long-term effects on host fitness—indeed "natural pruning" of branches and heartrot has sometimes been regarded as beneficial (Peace, 1962; Janzen, 1976); lack of definite evidence that apparent responsiveness resulting in the sealing off of functional

tissues is specifically towards "infection" rather than non-specifically towards damage and aeration (Boddy and Rayner, 1983a).

Here it is worth recalling that selectivity for particular plant taxa is by no means a unique feature of pathogenic fungi. It also occurs widely, although perhaps not with the specificity of gene-for-gene interactions, amongst mycorrhizal fungi forming mutualistic symbioses and indeed amongst many purely saprotrophic, non-pathogenic fungi colonizing dead plant remains (Rayner *et al.*, 1985). Here, a direct deleterious effect on plant fitness and consequent requirement for evolution of resistance mechanisms is obviated, so that selectivity must be due to other causes.

A more general way of understanding fungal distribution, already alluded to, is within the context of the three primary ecological strategies, ruderal, stress-tolerant and combative which are respectively conditioned by the three major environmental determinants, disturbance, stress and incidence of competitors (Cooke and Rayner, 1984; cf. Grime, 1977, 1978, 1979; Pugh, 1980; Andrews and Rouse, 1982). A simplified discussion of the relevant principles follows.

Fungi exhibiting ruderal strategies have an ephemeral existence associated with rapid colonization of habitats which are competitor-free due to recent disturbance; easily assimilable nutrients are absorbed and converted to reproductive biomass, allowing exit as competitors establish themselves. These fungi are hence characteristic either of ephemeral habitats or of early stages of colonization of durable ones. They tend to be non-selective, and as mentioned previously, *Chondrostereum purpureum*, *Corticium evolvens*, *Stereum sanguinolentum*, *Schizophyllum commune* and *Flammulina velutipes* provide examples of wood-decay species possessing at least some ruderal characteristics.

Stress-tolerant fungi are characteristic of undisturbed habitats which are relatively competitor-free because of the occurrence of conditions ("stress") unfavourable for the production of biomass by the majority of potential colonists. The essential feature of these fungi is therefore their close adaptation to a particular set of selective micro-environmental conditions and lack of competitiveness where other conditions obtain. This provides an obvious explanation for the selectivity of many tree-decay fungi, since the requisite set of conditions may be expected to predominate in one type of tree whilst occurring less frequently, if at all, in others.

Given that stress-tolerance characterizes many tree-decay fungi, several distinctive types of behaviour occur with respect to alleviation or alteration of the relevant selective conditions. In some cases activity may cease directly, and the fungus ultimately become replaced by others. Thus many heartrot fungi probably display almost pure stress-tolerant strategies, persisting as long as the selective conditions to which they are adapted are maintained, but failing to remain active for long in felled or fallen timber (Highley and Kirk, 1979).

They are predominantly slow-growing and are non-combative against other fungi in culture (Rypáček, 1966; Rayner and Hedges, 1982). Hence, they owe their long life span, and ultimately considerable extent (see above), largely to the durability of their hosts.

Fungi believed to have latent invasion strategies (see above) exhibit a different pattern of behaviour. Here alleviation of the selective conditions is immediately capitalized on by mycelial proliferation from previously cryptic inoculum, and results in a substantial competitive advantage in allowing rapid possession of the available domain, i.e. "primary resource capture" (see Cooke and Rayner, 1984; Rayner and Webber, 1984). This initial competitive advantage may subsequently be sustained by combative mechanisms enabling effective defence of the captured domain, or even further outgrowth therefrom, the fungus thus having a combination of stress-tolerant and combative characteristics (see below). *Daldinia concentrica* may provide an example of such behaviour, being able to defend against or even replace other potentially competitive decay fungi, and has been observed to persist probably for over twenty years in ash trunks whilst causing only moderate decay (Boddy *et al.*, 1985; A. D. M. Rayner and L. Boddy, unpublished). *Piptoporus betulinus* appears to be similarly combative, but the difficulty in establishing it, in the face of competition, from inoculations into cut stumps or even into standing trees, indicate that these combative characteristics are only expressed when it is firmly entrenched.

Other latent invaders may persist for a shorter period of time before being replaced by more combative fungi, and a priority for them is rapid allocation of the resources they command to reproduction. Thus they tend to combine stress-tolerant with ruderal characteristics. Amongst the fungi colonizing attached oak branches, for example, the pioneers *Stereum gausapatum*, *Vuillemimia comedens* and *Peniophora quercina* are subject to replacement by *Coriolus versicolor* and *Phlebia radiata* whilst the branches remain attached, or by mycelial-cord-forming fungi invading from the forest floor once the branches have fallen (Boddy and Rayner, 1983b; unpublished observations).

Fungi exhibiting purely combative strategies are characteristic of habitats which are relatively stress- and disturbance-free, so that success is dependent on effective defensive and/or attacking mechanisms allowing the maintenance of territory and/or the replacement of other fungi. Purely combative fungi are hence non-selective and would not normally be expected to initiate decay in standing trees, but as mentioned previously, some, such as *Bjerkandera adusta*, *Coriolus versicolor* and *Stereum hirsutum* may sometimes do so, perhaps via latent invasion mechanisms and predisposition.

Finally, the possibility must be mentioned that at least some of the evidence for selectivity might be misleading as a result of reliance on sporophore production for identification. There is now increasing evidence that many

fungi can develop as mycelium in substrata without necessarily subsequently fruiting, presumably with long-term deleterious effects on fitness unless some other means of reproduction or survival be adopted. Examples include certain wood-decay species which have been found in some very curious habitats. Thus a *Daldinia* sp. and *Hypoxylon serpens* have been found as endophytes in *Calluna* (Petrini, 1984). However, it is not clear whether or not these endophytes should be regarded as belonging to the same populations as their wood-decaying counterparts. *A priori*, the likelihood seems that they should not, partly based on some observations with other fungi. Thus in *Phomopsis oblonga* which invades elm (*Ulmus*) bark (see above), British populations have been found to contain two distinctive sub-populations. One of these (Group 1) is reproductively outcrossing, containing numerous unique, somatically incompatible genotypes. The other (Group 2) is reproductively non-outcrossing and clonal so that different isolates appear identical or very similar and are somatically compatible in culture. The two types are reproductively isolated (Brayford, 1983). A similar situation may occur in *Hypoxylon serpens*, where a preliminary study (Dowson, 1982) indicated that wood-decaying forms are reproductively outcrossing, contrasting with a strain isolated from soil (Barron, 1972) which is non-outcrossing and directly produces perithecial stromata yielding homogeneous progeny sets in culture. Somewhat analogous patterns are also present in *Ceratocystis ulmi* populations (Brasier, this volume).

These last considerations introduce the next major issue.

B. Adaptation, Diversification and the Correlation between Reproductive and Ecological Strategies

As just indicated, a major problem in understanding selectivity is the tendency to base discussion on observations of the distribution of *species* rather than populations. This tendency, which is a direct consequence of the neglect of population studies in mycology, obscures the possibility of adaptation to different niches and consequent diversification, as occurs amongst different *formae speciales* and indeed physiologic races of certain obligate necrotrophs and biotrophic plant pathogens. As a result both apparent non-selectivity and selectivity could sometimes effectively be taxonomic artefacts (Rayner *et al.*, 1985). Thus apparent non-selectivity could sometimes be the result of ecological specialization within the species resulting in diversification into one or more niche-adapted sub-populations. Equally, selectivity could sometimes be an artefact of narrow taxonomic delimitation whereby populations occurring in different habitats are described as different species, based on minor morphological differences and without evidence as to whether they belong to the same or different breeding populations. A brief discussion now

follows of the extent to which the limited number of population studies of tree decay fungi, so far available, can elucidate these issues.

Firstly, there is some evidence that certain morphologically similar but apparently host-adapted populations described as different species are indeed reproductively isolated. Several examples are provided in reviews by Burnett (1965, 1975, 1976, 1983), one of the clearest being in three North American species of *Peniophora*. One of these, *P. populnea* is confined to *Populus*, while a similar but distinct species *P. heterocystidea* occurs more widely on a range of deciduous trees. A third species *P. mutata* contains two intersterile sub-populations, one confined to *Populus*, and the other ranging onto other broad-leaved trees (McKeen, 1952). A rather similar situation probably occurs with other *Peniophora* spp. in Europe and Asia (E. Parmasto, personal communication). *P. quercina* ssp. *quercina* is widespread, but strongly selective for oak (*Quercus*), occurring only occasionally on chestnut (*Castanea*) and rarely on beech (*Fagus*). A very similar species *P. rufomarginata*, which has distinctly smaller basidiospores, is reproductively isolated from *P. quercina* and is selective for lime (*Tilia* spp.). *P. quercina* ssp. *caucasica* has spores of intermediate size, and is compatible with ssp. *quercina*. A fourth population, a new species, occurs on oak in Japan and the Far East and has very small spores.

The recent discovery of intersterile populations ("biological species"), see above) in *Armillaria* has also provided some evidence of ecological diversification (Rishbeth, 1982). Thus in England it has been found that *A. mellea ss. stricto* is a virulent pathogen of both coniferous and deciduous trees, but more particularly the latter. *A. ostoyae* is a pathogen particularly of conifers, but has also been detected in roots of suppressed oak (*Quercus robur*) trees (Thompson and Boddy, 1983). *A. bulbosa* is a widespread highly rhizomorphic species which is relatively non-pathogenic and occurs in trees weakened by stress or infection and also causes extensive butt rot in some broad leaved trees. *A. tabescens* is relatively uncommon and was virtually non-pathogenic in tests against small pines (*Pinus* spp.). A single collection of *A. cepestipes f. pseudobulbosa* also appeared to be non-pathogenic in such tests. Recently the sixth of the species recorded in Europe (Korhonen, 1978), *A. borealis* has been found in Scotland, and probably has a northern distribution (Gregory and Watling, 1985; Marxmuller, 1982). It occurs on both deciduous and coniferous trees, but birch may be a common native host.

The alternative issue, whether or not populations of the same species occurring on different hosts belong to the same or different gamodemes (breeding populations) seems rarely to have been investigated, although a good early example was set by Verrall (1937) with *Phellinus igniarius*. An important study which did indicate some evidence of divergence was that of Duncan and Macdonald (1967) with *Hirneola auricula-judae*. European populations, which are selective for elder (*Sambucus niger*) are geographically and

genetically isolated from North American populations. The latter in turn are divided into two sub-populations, one selective for deciduous trees, the other for coniferous trees, which are partially intersterile. More recently, Korkonen (1978b) has found evidence of intersterility associated with adaptation to *Pinus* and *Picea* hosts in *Heterobasidion annosum*.

The contrasting situation, the occurrence of the same gamodeme in different host trees has been demonstrated in British populations of *Stereum rugosum* and *S. gausapatum* (A. M. Ainsworth, personal communication). *S. rugosum* is especially found on coppiced trees, notably hazel (*Corylus avellana*) but can also be found on a variety of others. Interfertility has been demonstrated between collections on hazel, alder (*Alnus glutinosa*), birch (*Betula* sp.), cherry laurel (*Prunus laurocerasus*), *Rhododendron ponticum*, beech (*Fagus sylvatica*), crack willow (*Salix fragilis*), oak (*Quercus*) and holly (*Ilex aquifolium*). In *S. gausapatum* which is selective for oak (see above), members of the same gamodeme have also been detected in hazel and beech.

Occurrence of the same gamodeme in different trees does not, however, preclude the possibility of adaptation and consequent polymorphism within the population. Indeed, some evidence for host specialization, where isolates are more virulent towards the tree species from which they were obtained than against other tree species, has been obtained with *Heterobasidium annosum* (Worrall, Parmeter and Cobb, 1983). Equally, the very different selective conditions which may operate within the same tree might be expected to promote polymorphism. Herein, the considerable variation in mycelial characteristics which has been detected in several tree decay fungi, for example, *Piptoporus betulinus* (Adams, 1982); *Stereum gausapatum* (Herrick, 1939; Boddy and Rayner, 1982), and *Hypoxylon rubiginosum* (Whalley and Greenhalgh, 1971) may be significant, especially when these contrast markedly with the relative morphological uniformity of their sporophores. The reverse situation is shown by some non-selective, combative species, for example *Coriolus versicolor*, where considerable cultural uniformity of the dikaryons contrasts with the variation displayed by monokaryons and by fruit bodies (Williams, 1982).

A possible example of a change of ecological strategy underlying reproductive isolation, as opposed to a change in host preference *per se*, has been detected in two closely similar, but distinctive species of *Phlebia*, *P. radiata* and *P. rufa* (Boddy and Rayner, 1983b). *P. radiata* is a widespread, combative colonizer of wood from a wide range of deciduous trees; if found on standing trees there is usually good evidence that it acts as a secondary colonist, invading wood already occupied by pioneer decay fungi. One of these pioneers is *P. rufa*, which favours large light-suppressed branches, particularly of oak (*Quercus*) but also of beech (*Fagus sylvatica*) where it forms extensive individual genotypes. A strong somatic rejection response occurs, *following*

hyphal fusion, between both homokaryons and heterokaryons of the two fungi, which are intersterile. These differences are reflected in their different cultural parameters: *P. rufa* is less combative against other fungi and more likely to fruit than *P. radiata* and also seems to possess an only partially effective mating system; there is thus evidence that it is moving towards a stress-tolerant-ruderal latent invasion strategy (cf. above).

The partial breakdown of the mating system evident in *P. rufa* introduces another important possibility; that there may be some correlation between ecological strategy and breeding biology. In flowering plants there is evidence for a strong correlation between ruderal strategies and non-outcrossing (apomictic) populations (Briggs and Walters, 1984), and it would make sense if the same tendency was found amongst fungi, an ephemeral existence under non-selective conditions obviously reducing the requirement for adaptation. Here, the non-outcrossing behaviour of *Stereum sanguinolentum* mentioned previously in connection with its apparently ruderal or stress-tolerant-ruderal strategy in conifers is of particular interest, and *Stereum rameale* appears to be its counterpart on deciduous trees. Of further interest is the occurrence of non-outcrossing in strains which are on the limit of the geographical distribution of the species, a situation also found in higher plants. This situation may occur in *Stereum hirsutum*, where it has been found that Scandinavian collections of the fungus are non-outcrossing, whereas British collections are outcrossing (Rayner *et al.*, 1984). Furthermore, strains of *Stereum subtomentosum* which have a more northern distribution than the very closely similar species *S. insignitum*, have so far been found to be non-outcrossing, whereas those of *S. insignitum* are outcrossing (A. M. Ainsworth, personal communication).

REFERENCES

Adams, D. H. (1974). *Norwest Sci.* **48,** 21–28.

Adams, D. H. and Roth, L. F. (1967). *Can. J. Bot.* **45,** 1538–1589.

Adams, D. H. and Roth, L. F. (1969). *For. Sci.* **15,** 327–331.

Adams, T. J. H. (1982). "*Piptoporus betulinus*, some aspects of population biology". Ph.D. Thesis, University of Exeter, Exeter.

Adams, T. J. H., Todd, N. K. and Rayner, A. D. M. (1981). *Trans. Brit. Mycol. Soc.* **76,** 510–513.

Anderson, J. B., Ullrich, R. C., Roth, L. F. and Filip, G. M. (1979). *Phytopathology* **69,** 1109–1111.

Anderson, N. A., Ostry, M. E. and Anderson, G. W. (1976). *U.S. For Serv. Res. Note* NC/214.

Andrews, J. H. and Rouse, D. I. (1982). *Amer. Nat.* **120,** 283–296.

Barrett, D. K. and Uscuplic, M. (1971). *New Phytol.* **70,** 581–598.

Barron, G. L. (1972). "The genera of Hyphomycetes from soil". Krieger Publishing Co., Huntington, New York.

Bier, J. E. (1959). *Can. J. Bot.* **37,** 229–238.
Bier, J. E. (1961). *Can. J. Bot.* **39,** 139–144.
Boddy, L., Gibbon, O. M. and Grundy, M. (1985). *Trans. Brit. Mycol. Soc.* **85,** 201–211.
Boddy, L. and Rayner, A. D. M. (1981). *Ann. Bot.* **47,** 271–274.
Boddy, L. and Rayner, A. D. M. (1982). *Trans. Brit. Mycol. Soc.* **78,** 337–351.
Boddy, L. and Rayner, A. D. M. (1983a). *New Phytol.* **94,** 623–641.
Boddy, L. and Rayner, A. D. M. (1983b). *Trans. Brit. Mycol. Soc.* **80,** 437–448.
Boddy, L. and Rayner, A. D. M. (1983c). *New Phytol.* **93,** 77–88.
Boddy, L. and Rayner, A. D. M. (1984a). *New Phytol.* **98,** 155–164.
Boddy, L. and Rayner, A. D. M. (1984b). *Trans. Brit. Mycol. Soc.* **82,** 501–505.
Boidin, J. (1971). *In* "Evolution in the higher Basidiomycetes" (R. H. Petersen, ed.), pp. 129–148. University of Tennessee Press, Knoxville.
Boidin, J. and Lanquentin, P. (1984). *Bull. Soc. Myc. Fr.* **100,** 211–236.
Boyce, J. S. (1961). "Forest pathology", McGraw-Hill, New York, Toronto and London.
Brasier, C. M. (1984). *In* "The ecology and physiology of the fungal mycelium" (D. H. Jennings and A. D. M. Rayner, eds), pp. 451–497. Cambridge University Press. Cambridge.
Brayford, D. (1983). "*Phomopsis oblonga* as a biological control agent of Dutch elm disease". Ph.D. Thesis, University of Wales, Aberystwyth, Wales.
Briggs, D. and Walters, S. M. (1984). "Plant variation and evolution", 2nd ed. Cambridge University Press, Cambridge.
Burnett, J. H. (1965). *In* "Incompatibility in fungi" (K. Esser and J. R. Raper, eds). pp. 98–113. Springer-Verlag, Berlin.
Burnett, J. H. (1975). "Mycogenetics". Wiley, London and New York.
Burnett, J. H. (1976). "Fundamentals of mycology", 2nd ed. Edward Arnold, London.
Burnett, J. H. (1983). *Trans. Brit. Mycol. Soc.* **81,** 1–14.
Bushnell, W. R. and Rowell, J. B. (1981). *Phytopathology* **71,** 1012–1014.
Campbell, A. H. (1938). *Trans. Brit. Mycol. Soc.* **22,** 151–159.
Cartwright, K. St. G. and Findlay, W. P. K. (1958). "Decay of timber and its prevention", 2nd ed. HMSO, London.
Chase, T. E. and Ullrich, R. C. (1983). *Mycologia* **75,** 825–831.
Childs, T. W. (1963). *Phytopathology* **53,** 1124–1127.
Coates, D. (1984). "The biological consequences of somatic incompatibility in wood decaying Basidiomycetes and other fungi". Ph.D. Thesis, University of Bath, Bath.
Coates, D. and Rayner, A. D. M. (1985a). *J. Gen. Micro.* **131,** 207–219.
Coates, D. and Rayner, A. D. M. (1985b). *Trans. Brit. Mycol. Soc.* **84,** 527–530.
Coates, D., Rayner, A. D. M. and Todd, N. K. (1981). *Trans. Brit. Mycol. Soc.* **76,** 41–51.
Coates, D., Rayner, A. D. M. and Boddy, L. (1985). *New Phytol.* **99,** 473–483.
Cooke, R. C. and Rayner, A. D. M. (1984). "Ecology of saprotrophic fungi". Longmans, London and New York.
Dowson, C. G. (1982). "Mycelial ecology of the Xylariaceae". Project report, University of Bath, Bath.
Duncan, E. G. and Macdonald, J. A. (1967). *Mycologia* **59,** 803–818.
Esser, K. and Meinhardt, F. (1984). *In* "Encyclopedia of plant physiology, Vol. 17" (H. F. Linskens and J. Heslop-Harrison, eds), pp. 350–361. Springer-Verlag. Berlin, Heidelberg, New York and Tokyo.
Etheridge, D. E. and Craig, H. M. (1976). *Can. J. For. Res.* **6,** 299–318.

Gammerman, A. F., Shupinskaya, M. D. and Yatsenko-Kamelevskii, A. A. (1963). "Medical plants: Healing plants of our country". Moscow.
Garrett, S. D. (1970). "Pathogenic root-infecting fungi". Cambridge University Press, Cambridge.
Gibbs, J. N. and Gulliver, C. C. (1977). *Eur. J. For. Pathol.* **7,** 193–200.
Gregory, P. H. (1984). *Trans. Brit. Mycol. Soc.* **82,** 1–11.
Gregory, S. C. and Watling, R. (1985). *Trans. Brit. Mycol. Soc.* **84,** 47–55.
Grime, J. P. (1977). *Amer. Nat.* **111,** 1169–1194.
Grime, J. P. (1978). *Symposium of British Ecological Society* **20,** 123–139.
Grime, J. P. (1979). "Plant strategies and vegetation processes". Wiley, Chichester and New York.
Hartig, R. (1874). "Wichtige Krankheiten der Waldbaume". Springer-Verlag, Berlin.
Hartig, R. (1878). "Die Zerzetzungerscheinungen des Holzes der Nadel holzbaume und der Eiche", Berlin.
Heath, M. C. (1981). *Phytopathology* **71,** 1121–1123.
Herrick, J. A. (1939). *Phytopathology* **29,** 504–511.
Highley, T. L. and Kirk, T. K. (1979). *Phytopathology* **69,** 1151–1157.
Hillis, W. E. (1977). *In* "The structure, biosynthesis and degradation of wood" (F. A. Loewus and V. C. Runeckles, eds), pp. 247–309. Plenum Press, New York and London.
Janzen, D. H. (1976). *Biotropica* **8,** 110.
Käärik, A. A. (1974). *In* "Biology of plant litter decomposition" (C. H. Dickinson and G. J. F. Pugh, eds), Vol. I, pp. 129–174. Academic Press, London and Orlando.
Kile, G. A. (1983). *Aust. J. Bot.* **31,** 657–671.
Korhonen, K. (1978a). *Karstenia* **18,** 31–42.
Korhonen, K. (1978b). *Commun. Inst. For. Fenn.* **94,** 1–25.
Lonsdale, D. (1983). *Yearbook Int. Dendr. Sol. 1982*, 90–97.
Lyman, J. C. and Ellstrand, N. C. (1984). *Heredity* **53,** 1–10.
Macdonald, J. A. (1937). *Ann. Appl. Biol.* **24,** 289–310.
McKeen, C. (1952). *Can. J. Bot.* **30,** 764–787.
Marxmuller, H. (1982). *Bull. Soc. Mycol. Fr.* **98,** 87–124.
Mercer, P. C. (1982). *In* "Decomposer Basidiomycetes: Their biology and ecology" (J. C. Frankland, J. N. Hedger and M. J. Swift, eds), pp. 143–160. Cambridge University Press, Cambridge.
Michaelopoulos-Skarmoutsis, H. (1980). "Fungi associated with decay of standing birch in Scotland". Ph.D. Thesis, University of Aberdeen, Aberdeen.
Ouchi, S. (1983). *Ann. Rev. Phytopathol.* **21,** 289–315.
Peace, T. R. (1962). "Pathology of trees and shrubs". Clarendon Press, Oxford.
Petrini, O. (1984). *Trans. Brit. Mycol. Soc.* **83,** 510–512.
Pugh, G. J. F. (1980). *Trans. Brit. Mycol. Soc.* **75,** 1–14.
Rayner, A. D. M. (1976). *Trans. Brit. Mycol. Soc.* **67,** 546–549.
Rayner, A. D. M. (1977). *Trans. Brit. Mycol. Soc.* **69,** 303–312.
Rayner, A. D. M. (1978). *Ann. Appl. Biol.* **89,** 131–134.
Rayner, A. D. M. (1979). *New Phytol.* **82,** 505–517.
Rayner, A. D. M., Coates, D., Ainsworth, A. M., Adams, T. J. H., Williams, E. N. D. and Todd, N. K. (1984). *In* "The ecology and physiology of the fungal mycelium" (D. H. Jennings and A. D. M. Rayner, eds), pp. 510–540. Cambridge University Press, Cambridge.
Rayner, A. D. M. and Hedges, M. J. (1982). *Trans. Brit. Mycol. Soc.* **78,** 370–373.

Rayner, A. D. M. and Todd, N. K. (1979). *Adv. Bot. Res.* **7,** 333–420.
Rayner, A. D. M. and Turton, M. N. (1982). *Trans. Brit. Mycol. Soc.* **78,** 483–493.
Rayner, A. D. M. and Webber, J. F. (1984). *In* "The ecology and physiology of the fungal mycelium" (D. H. Jennings and A. D. M. Rayner, eds), pp. 383–417. Cambridge University Press, Cambridge.
Rayner, A. D. M., Watling, R. and Frankland, J. C. (1985). *In* "Developmental biology of higher Basidiomycetes" (L. A. Casselton, D. Moore, D. A. Wood and J. C. Frankland, eds), pp. 1–40. Cambridge University Press, Cambridge.
Reid, D. A. (1976). *Trans. Brit. Mycol. Soc.* **67,** 329–332.
Rishbeth, J. (1951a). *Ann. Bot.* **15,** 1–21.
Rishbeth, J. (1951b). *Ann. Bot.* **15,** 221–246.
Rishbeth, J. (1963). *Ann. Appl. Biol.* **52,** 63–77.
Rishbeth, J. (1982). *Plant Pathol.* **31,** 9–17.
Roth, L. F. (1952). *Phytopathology* **42,** 518–519.
Rypácek, V. (1966). "Biologie Holzzerstorender Pilze". Fischer, Jena.
Scheffer, T. C. and Cowling, E. D. (1966). *Ann. Rev. Phytopathol.* **4,** 147–170.
Shaw, C. G. and Roth, L. F. (1976). *Phytopathology* **66,** 1210–1213.
Shigo, A. L. (1966). *U.S. Dept. Agr. For. Serv. Res. Paper* No. NE–43.
Shigo, A. L. (1967). *Int. Rev. For. Res.* **2,** 237–299.
Shigo, A. L. (1979). *U.S. Dept. Agr. For. Serv. Agr. Info. Bull.* No. 419.
Shigo, A. L. and Marx, H. G. (1977). *U.S. Dept. Agr. For. Serv. Agr. Info. Bull.* No. 405.
Shigo, A. L. and Shortle, W. C. (1979). *Phytopathology* **69,** 710–711.
Shortle, W. C. and Cowling, E. B. (1978). *Phytopathology* **68,** 617–623.
Tepper, C. S. and Anderson, A. J. (1984). *Phytopathology* **74,** 1143–1145.
Thomas, A. C., Mathee, F. N. and Hadlow, J. (1978). *The Deciduous Fruit Tree Grower* **28,** 92–98.
Thompson, W. (1984). *In* "The ecology and physiology of the fungal mycelium" (D. H. Jennings and A. D. M. Rayner, eds), pp. 185–214. Cambridge University Press, Cambridge.
Thompson, W. and Boddy, L. (1983). *New Phytol.* **93,** 277–291.
Thompson, W. and Rayner, A. D. M. (1982). *Trans. Brit. Mycol. Soc.* **78,** 193–200.
Tolmsoff, W. J. (1983). *Ann. Rev. Phytopathol.* **21,** 317–340.
Toole, R. E. (1961). *For. Sci.* **7,** 218–226.
Ullrich, R. C. and Anderson, J. B. (1978). *Experimental Mycology* **2,** 119–129.
Vanin, S. T. (1922). *J. Certr. Phyt. Stat. Chief. Bot. Card. Russ. Rep.* **11,** 9–23.
Verrall, A. F. (1937). *Tech. Bull. Minn. Agric. Exp. Sta.* No. 117.
Webber, J. F. and Brasier, C. M. (1984). *In* "Invertebrate-microbial interactions" (J. M. Anderson, A. D. M. Rayner and D. W. H. Walton, eds), pp. 217–306. Cambridge University Press, Cambridge.
Webber, J. F. and Gibbs, J. N. (1984). *Trans. Brit. Mycol. Soc.* **82,** 348–352.
Whalley, A. J. S. and Greenhalgh, G. N. (1971). *Trans. Brit. Mycol. Soc.* **65,** 369–373.
Whalley, A. J. S. and Watling, R. (1980). *Trans. Brit. Mycol. Soc.* **74,** 399–406.
Whalley, A. J. S. and Watling, R. (1984). *Bull. Brit. Mycol. Soc.* **18,** 126–127.
Williams, E. (1982). "Population Studies with *Coriolus versicolor*". Ph.D. Thesis, University of Exeter, Exeter.
Woodgate-Jones, P. (1982). Ph.D. Thesis, University of Bristol, Bristol.
Worrall, J. J., Parmeter, J. R. and Cobb, F. W. (1983). *Phytopathology* **73,** 304–307.